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PRIMITIVE GENETIC MECHANISMS AND THE ORIGIN OF CHROMOSOMES

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INTRODUCTION

Discussion of the origin of life has enjoyed a recent revival. While of necessity no less speculative than the treatments of twenty and thirty years ago, recent thinking has had the benefit of considerably increased knowledge of the molecular basis of metabolism and of a growing body of experimental data bearing on the spontaneous synthesis of organic compounds. These successes have very naturally directed attention to the primary steps in the origin of life leading from the elements, free radicals and simple compounds assumed to be present in the pre-biotic earth to the formation of a variety of organic compounds of the polypeptide or nucleotide level of complexity. The problems involved in reconstructing these steps represent but the first stage of a succession of problems of the origin of life, which may be somewhat arbitrarily divided as follows:

1. abiogenesis of organic molecules;
2. aggregation of organic molecules into metastable localized droplets;
3. evolution of anabolic coupled-reaction systems and enzymes, leading to auto-catalytic growth;
4. evolution of mechanisms controlling replication and leading to ordered division. It is only with the acquisition of such mechanisms for genetic stability, necessary for protection of the integrity of the system, that the droplet achieves the status of a *cell.*

A number of proposals of possible steps in stage 1 have been made recently (reviewed by Oparin, 1957, and in Nigrelli et al, 1957). Although geochemists are not yet agreed as to the composition of primitive earth envelopes and there is also room for divergence of opinion regarding the most likely energy sources for primary spontaneous syntheses, no serious obstacle appears to lie in the way of accepting the hypothesis that a variety of organic molecules could have accumulated in quantity in pre-biotic times. Recent work has shown that the non-biological synthesis of amino acids, pyrroles, etc. by a number of different methods is a laboratory practicality and hence a historical possibility. Whichever of these re-

actions proves most acceptable — and perhaps several were involved in different places or at different stages — this evolutionary level appears to present the least difficulty of the four.

Stage 2 has been discussed by a number of authors, including Oparin (1957), Pringle (1953, 1954), and Sagan (1957). Mechanisms for the concentration of organic molecules and for their aggregation appear to have been available. These include coacervation (Oparin, 1957), diurnal temperature cycles (Kavanau, 1947; Sagan, 1957), differential adsorption (Bernal, 1949), and stationary wave patterns of concentration (Turing, 1952; Pringle, 1954).

There is another aggregation mechanism that does not appear to have been considered in previous discussions of the origin of life, and that provides a means for concentrating organic substances. *Inclusion compounds* are formed by substances that crystallize with channel-like or cage-like spaces in which a "guest" compound can be enclosed in a stable union without chemical bonding between the two (Baron, 1957). Inclusion compounds have a number of properties that make them interesting in connection with this stage of pre-biotic evolution:

1. They are versatile, a given compound being able to accommodate a variety of guests. The limitation is not so much chemical as spatial; the included compound must have appropriate characteristics of geometry, size, and, in some instances, steric configuration.

2. They are stable, and their stability comes from non-specific forces such as van der Waals forces and electrostatic attraction.

3. Enclosure within the channels of the host confers protection on the guest compound from external influences. For example, a chain of unsaturated fatty acid may be enclosed in urea in the form of a stable inclusion compound. In this state it is stable to oxidation.

4. Hosts that form channel-like spaces can enclose guest chains of indefinite length. Such chains would be protected from depolymerization by external agents.

5. The selective action of inclusion compound hosts endows them with the ability to remove guest molecules from solution, thus conceivably accelerating the rate of reactions providing such guests. Conversely, with destruction of the cage by heat or otherwise, large concentrations of guest material would be locally released.

6. Some host compounds can selectively take up preferred optical isomers. The characteristic optical activity of components of the living organism has often been commented on (Goldschmidt, 1952). Wald (1957) has argued for the selective advantage of polymers of uniform optical configuration over DL polymers. Resolution of racemic mixtures by inclusion compounds would provide a way in which optically active molecules of the same configuration could have been locally concentrated.

Bernal (1949, 1954) has for some time championed the idea that clays may have provided adsorptive surfaces on which primitive life components were concentrated. In the light of this suggestion, possible naturally

occurring hosts that deserve special attention are the zeolites, which form channel-like spaces, and the bentonites, which form stratified structures capable of including compounds with polar groups between their lamellae.

Stage 3 has been discussed by Calvin (1956) and by Allen (1957). Both authors adopt a gradualistic view of the origin of self-catalyzing systems. Calvin's arguments are directed towards nucleic acids and phosphorylation mechanisms as important elements of such systems. Allen's more general treatment invokes any chain of reactions in which a product catalyzes the formation of a precursor in the chain ("reflexive catalysis").

Relatively few authors have dealt with stage 4 despite the fact that at this level lie some of the more perplexing problems in the way of a satisfactory theory of the origin of life. Boyden (1953), Dodson (1953), Crosby (1955) and Lindegren (1957) have addressed themselves to the question of how primitive reproductive mechanisms evolved.

This paper will concern itself with the problem of the evolution of genetic stability, a crucial one for the establishment of life as a continuous manifestation rather than a fleeting and fragile phenomenon.

It is a pleasure to record my debt to Drs. J. Singer, L.N. Howard, and K.C. Atwood for helpful suggestions and stimulating discussion.

AMITOTIC REPRODUCTION

Most present-day organisms have a relatively small number of chromosomes, the integrity and number of which are preserved by the controlled synthesis of replicas and by an elaborate mitotic mechanism. With the exception of polyploid and polytene tissues (for example, as in Amphibia and Diptera), the synthesis of genetic material is followed by orderly separation of the products. The exceptions cited are better regarded as stabilized modifications of the process than as representing a breakdown in the mechanism of control.

The features which make asexual reproduction successful are complex phenomena including:

1. a mitotic apparatus (spindle-kinetochore-centrosome system);
2. linkage of genes into chromosomes;
3. synchronization of chromosome duplication;
4. restriction of chromosome synthesis to once per division cycle;
5. segregation of the genetic apparatus from the general metabolic apparatus by a nuclear membrane.

How did this complex nucleo-cytoplasmic mechanism arise? Speculations on questions like this, where experimental tests do not immediately suggest themselves, are apt to be too unbridled to be useful. It is nevertheless fruitful to examine the modes of reproduction open to a primordial organism devoid of these specializations. These restrictions have interesting implications which must be taken into account in any attempt to reconstruct the early history of life. Moreover, these implications may

have some heuristic value in view of the variety of genetic mechanisms now known to exist in the microbiological world.

A number of writers (Muller, 1947, 1955; Calvin, 1956; Sagan, 1957) have pictured the ancestral organism as a free-living naked gene that evolved by increasing the number of its functions. Lindegren (1957) has criticized this conception on the ground that genes as we know them are not self-reproducing entities, it being rather the chromosome-cell system as a whole that reproduces. He considers the chromosomes to be no more autonomous than other cellular organelles, and presents the very interesting possibility that genetic capacities originally in the cytoplasm may have been transferred secondarily to nuclear genes.

On either the "naked gene" or "anucleate cell" hypothesis, it seems clear that the early organism must have gone through a stage when "genic" and "cytoplasmic" components were present, but with the genic material not necessarily segregated in a nucleus or organized into chromosomes. The length of time that would have been required for the evolution of mitosis is open to some questions. Boyden (1953) believes that it must have taken a period "perhaps of the order of magnitude of hundreds of millions of years." Crosby (1955) takes issue with this estimate. He correctly points out that evolutionary rates should be measured in generations rather than years, and that micro-organisms have a short generation time. Taking two hours as the generation time (more likely an over- than an under-estimate, according to Crosby) this would make 5,000 generations a year, which would allow time a great deal of evolutionary change.

At all events, the important question is not one of physical time, but of biological time. Whether it took centuries or millenia, we must assume a stage lasting thousands of cell generations during which reproduction somehow took place prior to the refinement of a mitotic cycle. Surely this era constituted one of the major crises in the evolution of life.

To survive and grow, the protocell must have had a number of coupled reactions (probably relatively small on the heterotroph hypothesis) sufficient to capture energy and synthesize all the elements of the system. A simple assumption — but not a necessary one — consistent with the characteristics of later products of evolution is that each such function was mediated by a gene. The nature of the gene does not affect the argument. We shall picture it as a chain of nucleotides, single or double, and with or without a conjugated polypeptide chain.

What kind of genetic organization are we to postulate for these protocells? Any metastable droplet of the kind envisaged, operating as an open system, must have had several catalytic functions. The existence, *ab initio,* of a single chromosome, carrying a number of genes with related functions, is difficult to imagine. But, as can be shown, selective mechanisms can account for the *secondary* origin of chromosomes. I lean to the the view, therefore, that the more reasonable starting picture is that of a cell containing a variety of essential particles, each capable of being replicated or being acquired. These particles would be distributed to the

daughter cells at random during division, there being as yet no mitotic mechanism.

Division in a cell of this grade of evolution might have occurred when a critical mass was attained, either as a result of inner diffusive forces or from external turbulence (Oparin, 1957). Or, as Anderson (1956) has suggested, division might be triggered by a shift in polyelectrolyte balance resulting from different rates of synthesis of amino acids and nucleotides. Under any of these conditions, the timing of division might have been irregular, the size of the daughter cells may or may not have been equal, and the genetic particles would be carried to one or the other daughter cell at random.

As a consequence, the probability of loss of essential functions through misdivisions was very high. Assuming a "haploid" number of particles, division could never result in the survival of both daughter cells, and a high proportion of divisions would result in loss of at least one essential particle from both daughter cells. Such cells faced three possible fates: 1. early death and disintegration; 2. restriction of anabolic activity, but with metastability maintained. Such a cell might continue to survive as an auxotroph. Under conditions of high population density, cells with complementary losses might survive by cross-feeding. 3. Cells in this state might reacquire lost functions either by mutation or by chance coalescence with another cell. The formation of such heterozygotes (heterocaryonts) may have been very important in the early evolution of cells. This process is envisaged as a forerunner of sexuality, differing from the latter in lack of specificity.

But haploidy in present-day organisms is maintained by the mitotic cycle. With uncontrolled replication of genes, the cell would have contained various numbers of replicas of its different genetic particles. The success of reproduction would have been limited by the gene represented by the fewest replicas.

It will simplify the discussion to consider the reproductive potential in terms of an average number of replicas. If we assume that a cell contains n different particles each controlling an essential function, and k replicas of each particle, these kn particles can be distributed to two daughter cells of equal volume in 2^{kn} ways. If k is greater than one, each particle may be distributed in 2^k ways, of which two are lethal to one or the other daughter cell, and $2^k - 2$ ways lead to the survival of both progeny cells, because at least one replica is received by each cell. Hence, the total number of ways in which particles may be distributed to result in the survival of both daughter cells is $(2^k - 2)^n$.

The probability of successful divisions (survival of both daughter cells), which we will denote as P_s, is therefore given by:

$$P_s = \frac{(2^k - 2)^n}{2^{kn}}$$

which may be written:

$$P_s = \left(1 - \frac{1}{2^{k-1}}\right)^n \tag{1}$$

(If genes A, B, C, ... are represented by different numbers of replicas k_A, k_B, k_C, ..., then

$$P_s = \frac{(2^{k_A} - 2)\,(2^{k_B} - 2)\,(2^{k_C} - 2) \ldots}{2^{k_A + k_B + k_C \ldots}}) \tag{2}$$

Similarly, it can be shown that the probability that only one of the two daughter cells will receive a complete genome is

$$P_s' = 2\left[\left(1 - \frac{1}{2^k}\right)^n - \left(1 - \frac{1}{2^{k-1}}\right)^n\right] \tag{3}$$

As a result of such divisions, the cell number is not increased. Genetic balance may, however, be affected by changes in the distribution of k (aneuploidy of various sorts). The probability of complete lethality (P_l), each daughter cell being deficient for at least one gene, so that neither is viable, is

$$P_l = 1 - 2\left(1 - \frac{1}{2^k}\right)^n + \left(1 - \frac{1}{2^{k-1}}\right)^n \tag{4}$$

The population size of clones formed by cells dividing amitotically in this manner is given by

$$N_g = N_o\, g \log (1 + P_s - P_l) \tag{5}$$

where N_g is the population size after g generations and N_o is the initial population size. For low numbers of k, $(P_s - P_l)$ is negative, implying extinction of the clone. This means that even if the protocells had only a few different genes, they had to be polyploid to survive. Where $(P_s - P_l)$ is positive but small, the rate of population increase is slow, and probably insufficient to permit the establishment of effective population size for evolutionary advance, assuming mutation rates similar to those known today. Moreover, since initial population size was probably small, the variance of P_s and P_l was great enough to make extinction very likely.

It is evident that improved survival is attainable in two ways: increasing k (endopolyploidy) or decreasing n (linkage into chromosomes). A com-

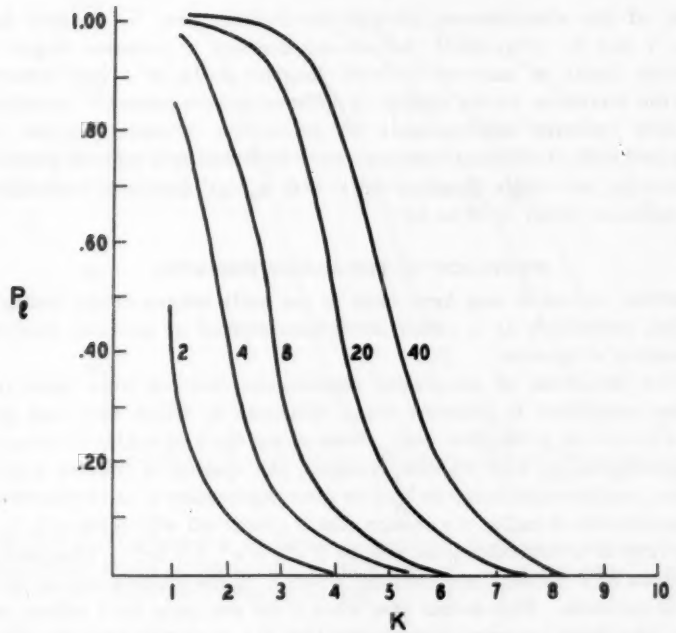

FIGURE 1. Probability of lethality to both progeny cells of an amitotic division (P_ℓ) as a function of replica number (k) for various numbers of essential particles (n = 2, 4, 8, 20, 40).

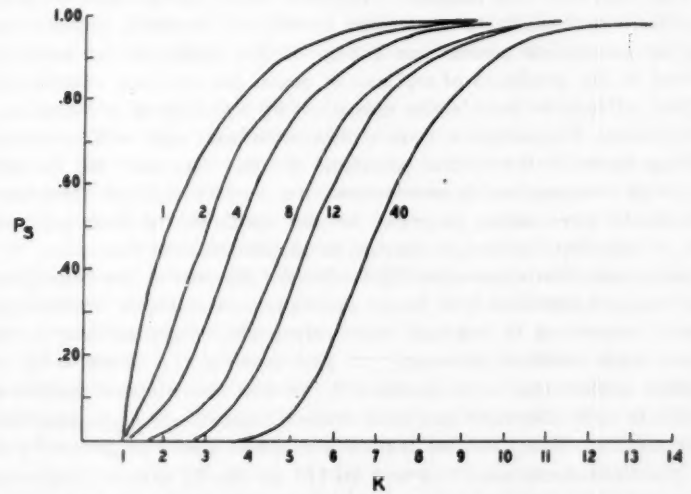

FIGURE 2. Probability of amitotic reproduction with survival of both daughter cells (P_s), as a function of replica number (k) for various numbers of essential particles (n = 1, 2, 4, 8, 12, and 40).

parison of the effectiveness of the two methods may be gleaned from figures 1 and 2. For small chromosome numbers a moderate degree of polyploidy leads to survival of both daughter cells in a high percentage of the divisions. As the number of different genetic particles increases, polyploidy becomes indispensable for successful amitotic division, but even a cell with 30 different functions, each mediated by a separate particle, can produce two viable daughter tells with a high degree of probability, if the minimum ploidy is 10 or 12.

POLYPLOIDY VS. CHROMOSOME FORMATION

Essential though it may have been in the early stages of the evolution of cells, polyploidy is a rather inefficient method of insuring survival, for a number of reasons.

1. The definition of successful reproduction that we have used is a minimum condition: it includes those divisions in which only one gene replica passes to a daughter cell. Even where the probability of successful reproduction is high by this criterion, the chance of loss of a given function remains significant as long as gene duplication is unsynchronized. In a population of cells, the chance that a given cell will receive 0, 1, 2, ...replicas of a particular gene will be $1/e^k$, k/e^k, $k^2/2e^k$...(the successive terms of a Poisson distribution) where k is the average ploidy of the gene in question. This means that when k for any gene falls below, say, 8, the likelihood becomes appreciable that the gene will be lost. Considering the population as a whole, there will always be a number of cells that have genes with precariously low k numbers.

2. The high degree of polyploidy required raises the question of metabolic efficiency, which we must next consider. Attaining genetic continuity by polyploidy means that a part of the metabolic apparatus is committed to the synthesis of replicas of genes *qua* replicas; that is, the likelihood of loss of function is minimized by building up a redundancy of information. The metabolic cost of this redundancy may well have been a limiting factor in the further evolution of life. Not only did the cell have a high deoxynucleotide requirement, but nucleic acid polymers once formed would have acted as traps for the synthesis of their replicas. Clearly a selective advantage attached to any reduction of this cost.

Computations from expression (1) lead quite directly to the conclusion that linkage of particles into larger aggregates of multiple functions is far more economical of material than polyploidy. Suppose there are 12 functions each mediated by a separate gene particle. To obtain a P_s of .95 would require that k be at least 9, so that the minimum number of particles in 108. Suppose now that these 12 genes are aggregated into 4 chromosomes. Four particles require a minimum k of 8 to give a P_s of .97. The "chromatin mass" is now 96 (12 for the 12 cistron lengths as before, times 8). If linked into three chromosomes, the 12 genes would need to be represented 7 times to give a P_s of .95, and the chromatin mass is now 84.

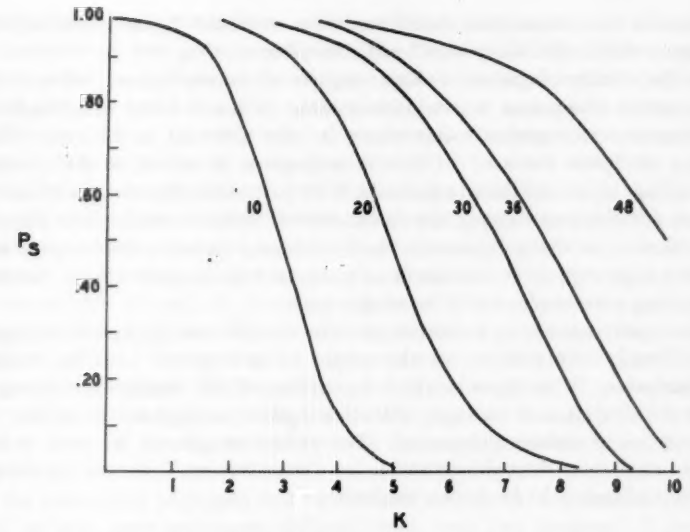

FIGURE 3. The influence of linkage on survival. Each curve represents probability of successful reproduction (P_s) for a constant "chromatin mass" (kn = 10, 20, 30, 36, 48) in various extents of linkage.

The efficiency thus resulting from linkage is shown in figure 3. The disparity in nucleic acid requirement between chromosome formation and polyploidy decreases as the number of essential functions increases. As the changing slope of the curves indicates, under conditions where the amount of nucleic acid is limiting, linkage confers the greatest selective advantage.

3. Another disability suffered by the amitotic cell is its lack of genic balance. The requirement for redundant gene replicas is statistical and bears no necessary relationship to the metabolic role of the gene product: —products needed in small concentration must be protected by as much genetic redundancy as those needed in larger amounts. As a result, in such systems, selection will favor the retention of "inefficient" genes, that is, genes whose individual contribution to metabolic activity is slight. This is so because if growth in any way depends on gene dosage, those genes that control the production of enzymes of low turn-over number or whose products are needed in larger amounts will be replicated repeatedly before division occurs, whereas genes that produce sufficient conditions for cell division in low dosage will be unable to build up a redundancy of replicas, unless "protected" by the presence of the former, less efficient type of gene. Under these conditions, and also because statistical fluctuations of aneuploidy were inevitable, viability was only possible where gene dosage was not critical. These considerations suggest that the primitive genetic controls were in all likelihood poly-

genic, in the sense that functions were mediated by multiple replicas of genes with individually small additive effects.

4. Polyploidy imposed a high degree of conservatism, because the segregation of mutants was relatively rare. In the absence of a Mendelian mechanism, segregation takes place by the binomial or Poisson distribution of "gene swarms." (This is analogous, in effect, to the situation prevailing in Mendelizing organisms with polygenic systems in which the genes are dispersed among the chromosomes; meiosis results in a binomial distribution of the polygenes.) In such a gene swarm a mutant gene must have a high degree of dominance to produce a phenotypic effect. Mutants enhancing prototrophy would be of this type.

The conclusion that primitive genetic control was polygenic mitigates considerably the problem of the origin of new genes (see for example Goldschmidt, 1958, for a critical discussion of the duplication theories). With the evolution of linkage, selection against oligogenes is relaxed and they come to replace polygenes. The redundant genetic material is thus made available through mutation (or "repatterning," if one prefers to follow Goldschmidt) for further evolution.

THE ORIGIN OF LINKAGE

It has been indicated that a number of selective forces favored linkage: (1) the chance of errors in reproduction was reduced. (2) Linkage resulted in greater economy of nucleic acid metabolism. (3) With random segregation of polygenes, additive effects produced a binomial distribution of polygenes. If such polygenes were advantageous, the selective advantage would be enhanced by linkage.

It remains to consider how linkages might have originated. A number of alternative ways can be suggested. (1) We might envisage that a polynucleotide chain increased in length by the terminal addition of nucleotides, in the manner suggested by the experimental results of Adler et al (1958). (2) The primitive cell might contain particles of various lengths and degree of complexity, and selection would favor the longer, multigenic chains. (3) The primarily unifunctional particles might become secondarily associated.

The first of these alternatives is open to the objection that this kind of step-wise addition requires us to assume either (improbably) that the new segment had immediate genetic significance, or that the new segment was retained despite its lack of selective value pending its ultimate mutation to a functional state. In this case, selection would favor shorter, not longer chains, with the non-genic nucleic acid being lost. The second alternative begs the question by assuming — again improbably — the prior existence of multigenic particles and still requires processes (1) and (3) for further increases in the length of the polymer.

We are thus led to examine the mechanisms by which secondary associations of genetic particles might arise. As long as the genetic coding is coextensive with the nucleotide chain, non-reciprocal processes (such as

transduction, gene conversion, translocation) are needed to account for the insertion of new genetic material into a chain. If the primitive gene particles had active as well as inactive sites, or contained repeats, crossing over would provide a means by which multigenic sequences could arise. Equal crossing over alone cannot, of course, increase chain length. This would have come about either by terminal additions or by classical inversion-crossovers resulting in duplications. (In the latter case, all such events would be effective, since in the pre-mitotic stage the problem of dicentric and acentric fragments does not arise.) It is not necessary to assume the evolution of meiosis or even mitosis prior to the occurrence of any of these processes. The occurrence of mitotic crossing over in Drosophila (Stern, 1936) and Aspergillus (Roper and Pritchard, 1955), the cytological demonstration of sister chromatid exchanges in Bellevalia (Taylor, 1958), and the phenomena of transduction and multiplicity reactivation in phage all point to the likelihood that crossing over is an inherent property of the genetic material, and hence primitive rather than a specialization restricted to the meiotic prophase.

In the pre-mitotic polyploid cell the several replicas of a genetic particle would in time have undergone differentiation from one another. If these particles had differing regions of genetic function and others of no selective value (either newly acquired "ends" or deleterious mutations) crossing over would put the two active sites on one particle and the reciprocal particle would become dispensable. In this way one particle becomes bifunctional, and n is reduced by 1.

A model for this process may be found in the Lewis effect, in which a double heterozygote in *trans* arrangement displays the mutant phenotype, while the *cis* arrangement is wild type. For example in the experiment of Roper and Prichard, Aspergillus heterozygous in *trans* for two adenine-requiring mutants produced adenine-independent recombinants by somatic crossing over. The creation of such a *cis* arrangement in a primordial auxotrophic cell would not only confer the selective advantage of prototrophy, but reduce n, since one of the two cross-over products becomes superfluous.

THE ORIGIN OF SEXUALITY

The selective mechanisms for the origin of chromosomes do not depend on sexuality. Nevertheless, the process would have been greatly facilitated by sexual recombination (see, for example, Muller, 1958).

It is widely assumed (Dodson, 1953; Darlington, 1958; Crosby, 1955) that sexuality must have evolved after the origin of mitosis. I can see no compelling reason for this assumption. The refinements of the bisexual system, meiosis and haplophase-diplophase alternation, do indeed depend upon the mitotic apparatus. But selective forces tending to promote cellular fusions would have been operative even in pre-mitotic stages.

A population of amitotic cells as we have described it would undergo random segregation, producing complementary auxotrophs, double loss

auxotrophs and prototrophs. Clones with ability to cross-feed would be selected for, producing symbiotic associations of high density (Horowitz, 1945; Crosby, 1955). In such a population the capacity for cellular fusion (at first probably promiscuous and non-specific) would have selective value, leading to the establishment of clones with enhanced capacity to fuse.

Primitively, the fertility factors thus selected for may have been replicated independently of other genes, like *F*, the transmissible fertility factor of *E. coli* (Lederberg, Cavalli, and Lederberg, 1952). A cytoplasmic factor might, however, be readily lost, as indeed *F* may be in some strains in which presumably it has a low rate of replication (Bernstein, 1958). Since clones of amitotic cells would suffer cell deaths (or produce auxotrophs) at the rate of $(1/2^{k-1})n$ per division, selection would favor the linkage of fertility factors into the chromosomes. We are thus led to a conclusion very much like Winge's old idea (1917) explaining sex on the basis of a heterozygous complementation of deficient functions.

SUMMARY

The statistical implications of the heterotroph hypothesis lead us to postulate a pre-mitotic sequence of stages in the early evolution of life in which

(1) polyploidy was a primitive condition that was replaced under selection pressure by lower conditions of ploidy;

(2) polygenic control of functions was replaced by oligogenic control, the redundant material being thus freed for new functions;

(3) unifunctional genetic particles were superseded by linked aggregates of genes, thus giving rise to chromosomes;

(4) selection for the ability of complementary auxotrophs to form heterocaryonts led to a primitive type of sexuality.

LITERATURE CITED

Adler, J., I. R. Lehman, M. J. Bessman, E. S. Simms and A. Kornberg, 1958, Enzymatic synthesis of deoxyribonucleic acid. IV. Linkage of single deoxynucleotides to the deoxynucleoside ends of deoxyribonucleic acid. Proc. Nat. Acad. Sci. 44: 641-647.

Allen, G., 1957, Reflexive catalysis, a possible mechanism of molecular duplication in prebiological evolution. Amer. Nat. 91: 65-78.

Anderson, N. G., 1956, Cell division. Quart. Rev. Biol. 31: 169-199.

Baron, M., 1957, Inclusion compounds. Org. Chem. Bull. 29: Nos. 2, 3.

Bernal, J. D., 1949, The physical basis of life. Proc. Phys. Soc. B 62: 597-618.

1954, The origin of life. New Biol. 16: 28-40.

Bernstein, H., 1958, Fertility factors in *Escherichia coli*. Symp. Soc. Exp. Biol. (Cambridge) 12: 93-103.

Boyden, A. A., 1953, Comparative evolution with special reference to primitive mechanisms. Evolution 7: 21-30.

Calvin, M., 1956, Chemical evolution and the origin of life. Amer. Sci. 44: 248–263.

Crosby, J. L., 1955, The evolution of mitosis. Proc. Univ. Durham Philos. Soc. 12: 73–81.

Darlington, C. D., 1958, The evolution of genetic systems. 2nd ed. Cambridge.

Dodson, E. O., 1953, Comment on the origin of sex and on meiosis. Evolution 7: 387–388.

Goldschmidt, R. B., 1958, Theoretical genetics. 563 pp. Berkeley and Los Angeles.

Goldschmidt, V. M., 1952, Geochemical aspects of the origin of complex organic molecules of the earth as precursors to organic life. New Biol. 12: 97–105.

Horowitz, N. H., 1945, On the evolution of biochemical syntheses. Proc. Nat. Acad. Sci. 31: 153–157.

Kavanau, J. L., 1947, Some physico-chemical aspects of life and evolution in relation to the living state. Amer. Nat. 81: 161–184.

Lederberg, J., L. L. Cavalli and E. M. Lederberg, 1952, Sex compatibility in *Escherichia coli*. Genetics 37: 720–730.

Lindegren, C. C., 1957, The role of the gene in evolution. Ann. N. Y. Acad. Sci. 69: 338–351.

Muller, H. J., 1947, Pilgrim Trust Lecture. The gene. Proc. Roy. Soc. London B 134: 1–37.

1955, Life. Science 121: 1–9.

1958, Evolution by mutation. Bull. Amer. Math. Soc. 64: 137–160.

Nigrelli, R. F., et al., 1957, Modern ideas on spontaneous generation. Ann. N. Y. Acad. Sci. 69: 255–376.

Oparin, A. I., 1957, The origin of life on earth. 495 pp. Edinburgh and New York.

Pringle, J. W. S., 1953, The origin of life. Symp. Soc. Exp. Biol. 7: 1–21.

1954, The evolution of living matter. New Biol. 16: 54–67.

Roper, J. A., and R. H. Pritchard, 1955, Recovery of the complementary products of mitotic crossing-over. Nature 175: 639.

Sagan, C., 1957, Radiation and the origin of the gene. Evolution 11: 40–55.

Stern, C., 1936, Somatic crossing-over and segregation in *Drosophila melanogaster*. Genetics 21: 625–730.

Taylor, J. H., 1958, Sister chromatid exchanges in tritium-labeled chromosomes. Genetics 43: 515–529.

Turing, A. M., 1952, The chemical basis of morphogenesis. Phil. Trans. Roy. Soc. B 237: 37–72.

Wald, G., 1957, The origin of optical activity. Ann. N. Y. Acad. Sci. 69: 352–368.

Winge, O., 1917, The chromosomes. Their number and general importance. C. R. trav. lab. Carlsberg 13: 131–275.

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EXPERIMENTAL STUDIES OF MIMICRY. IV. THE REACTIONS OF STARLINGS TO DIFFERENT PROPORTIONS OF MODELS AND MIMICS

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INTRODUCTION

One of the basic tenets of Batesian mimicry has been that in order for a mimetic color-pattern to evolve and be maintained, the model must occur in greater frequency than its mimic. This is because a vertebrate predator in learning to associate unpalatability with a specific color-pattern would presumably have more frequently to experience unpalatable individuals (the models) than palatable ones (the mimics). That the selective advantage of mimicry is reduced when the model species is rare, has been suggested for several African mimetic butterflies by Carpenter (1932), Ford (1936), Carpenter (1949), and reviewed by Sheppard (1959). These authors showed that in areas where, or times when, the model frequency was low, the degree of perfection of the mimetic pattern was much lessened. This phenomenon has come to be known as breakdown of mimicry and is also known to exist (from unpublished work) in the North American mimic butterfly, *Papilio troilus* L.

There is thus considerable indirect evidence in support of the idea that a higher frequency of models is necessary for the maintenance of mimicry in nature. Nevertheless, no experimental studies have been made to discover the effect of different proportions of models and mimics on the ability of predators to learn to reject them. The present study was therefore undertaken to investigate this problem with caged Starlings (*Sturnus vulgaris* (L.)) as predators, and mealworms (*Tenebrio molitor* L.) as artificial models and mimics.

THE BIRDS

The Starlings used in these experiments were trapped as adults at Milton, Berkshire, England, in the winter of 1957–1958 and were banded and released at the completion of the study. Eight bird cages were constructed, each measuring 24 inches wide × 30 inches high × 30 inches deep, with plywood sides, half inch wire mesh front, back, and top, and a galvanized steel tray floor. The front of each had a metal strip five inches high, across the base of the cage, in the middle of which was a sliding door through which experimental insects were introduced. The floors were lined with newspaper, and each cage had a plastic water bottle and a dish of P. Sluis Universal bird food, a commercial mixture imported from Holland. In addition, each bird was given grit, cuttlefish bone, and two drops of cod liver oil per day.

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Eight Starlings were trapped for each of two series of experiments and were caged individually. Because of the plywood sides and the positions of the cages, the birds could not see one another's reactions. Unlike the Scrub Jays of the previous studies on mimicry (Brower, 1958a, b, c), the Starlings were shy and required from two to three weeks to become tame enough to be used. In the first series, early in the taming period, two birds failed to eat the food provided and died. These were replaced and no further deaths occurred. However, all were not equally calm: of the eight in the first set, four were useable, and in the second group again only four of eight could be used, although a fifth was tame enough, but would not eat mealworms. Shyness did not appear to correlate with sex; in the second set there were two males and three females that were tame, and two males and one female that were shy. The characters used for determining the sex were taken from Witherby *et al.* (1938) and were: bill color, eye color, presence or absence of spotting and of sheen, and shape of feathers. All were adults in the second set except one first-winter male (bird 1). The sexes of the first set were not determined.

ARTIFICIAL MODELS AND MIMICS

In this investigation, mealworms colored by means of quick-drying cellulose paints were used for experimental food as a substitute for actual species of models and mimics. By applying a band of paint to the third and fourth abdominal segments with a small camel's hair brush, and allowing it to dry and become odorless, three categories of mealworms were made:

1. edibles: banded with orange and dipped into distilled water.
2. models: banded with green and dipped into a 66 per cent aqueous solution of quinine dihydrochloride.
3. mimics: banded with green and dipped into distilled water.

The purpose of the orange-banded edible mealworms was first to show that birds can associate orange, often a warning color in nature, with palatability, and second, to be certain that the paint itself was not unpalatable to the birds. The green paint was chosen for the unpalatable models because it is usually associated with protectively colored, highly edible insects, and therefore the birds probably would not have had a previously learned aversion to green. The mealworms were banded and treated according to the categories above before the start of each day's experiments. With this method, models and mimics were visually identical so that the mimic was "perfect."

PROCEDURE

The experimental procedure was based on a modification of that used in mimicry experiments with butterflies (Brower, 1958). For the first group of four Starlings four different proportions of green-banded model and mimic mealworms were selected, and each bird was assigned one.

A. 1 mimic: 9 models (ten per cent mimics).
B. 3 mimics: 7 models (30 per cent mimics).

C. 9 mimics: 1 model (90 per cent mimics).
D. A control bird (100 per cent mimics).

A table of random numbers was used to obtain randomness in the order of presentation of the mimics and models in each of the proportions for any given series of ten trials. For example, at 30 per cent mimics, the mimics were presented in the fourth, seventh, and eighth trial in one series of ten trials, third, fifth, and ninth in the next, *etc.*, until 16 sets of ten trials were completed. Thus the birds could not learn to predict the order of mimics and models. In addition to green-banded models and mimics, orange-banded edibles were also given to the Starlings, for the reasons stated above and to assure that they were hungry throughout the experiments. If a bird refused to eat an edible mealworm, the experiments were temporarily suspended until its appetite returned, and that trial was disqualified. As in the earlier work with butterflies, each trial consisted of offering a sequential pair of mealworms, one model *or* one mimic, and one edible to a bird. A random number table was again used to determine the order of presentation of each in such a way that runs of more than two of each kind were prevented, as fully described in the earlier paper (Brower, 1958a).

The random series for each proportion (ten per cent mimics, 30 per cent mimics, 90 per cent mimics, 100 per cent mimics) was determined prior to the experiments and the same sequences used with the first set of four Starlings were repeated for the second, with the addition of one new proportion, six mimics to four models (60 per cent mimics).

It had been planned that the Starlings would be introduced to their respective proportions of mimics and models at the outset of the first series of experiments. This was an attempt to simulate a natural situation in which a bird might be confronted with a population of models and mimics of a given relative frequency. However, there were initial difficulties in finding an odorless substance which was unpalatable enough to cause the birds to learn to reject the model mealworms on sight alone.

In these preliminary trials, solutions of sucrose octa-acetate, bitter aloes, a commercial bird repellant, and ten per cent and 20 per cent aqueous solutions of quinine dihydrochloride were all found to be insufficiently distasteful. But a 66 per cent solution of quinine dihydrochloride was so unpalatable to the Starlings that they soon learned to reject models on sight alone. By this time, they had already partially learned from the other unsuitable substances that model mealworms (green-banded) were less palatable than the orange-banded edibles. As a result of these difficulties, the birds of the first set of experiments were not introduced to their respective proportions of models and mimics until trial 61, whereas the second set of Starlings got the prescribed proportions of models and mimics from trial 1, as originally planned. In spite of this initial difference in the two groups, both were given a total of 160 trials with their respective proportions of models and mimics.

During an experiment, one banded mealworm at a time was placed on clean, white filter paper in a petri dish, after its head had been crushed with for-

ceps so that it would not walk. When it was immobile, the dish was put into a bird's cage through the sliding metal door. As soon as the dish was inside, I moved out of sight so that I could observe the bird and yet it could not see me. This was done because they were relatively shy, and in addition to reduce the possibility of a bird getting a cue as to the palatability of a mealworm from some inadvertent gesture or expression on my part. The complex behavior of the Starlings towards mimics, described below, very strongly indicates that they were not taking cues as to palatability from the experimenter.

Each mealworm was left in a cage for one minute during which time the bird might: 1) not touch it (NT); 2) peck it (P); 3) kill it (K); 4) eat it (E). The category of response and the reaction time of each bird were recorded, and general notes on its behavior during an experiment were kept. In the preliminary trials, edibles were seized in ten seconds or less by all the birds, as were mimics by the control bird of the first group, so that the refusal to touch a mealworm for one minute was considered ample as a criterion of rejection. On most days, each bird was given ten trials, that is, was presented with 20 mealworms, as each trial consisted of a randomized pair, one model *or* mimic, and one edible.

DATA

The first group of Starlings. During the first eight trials with 66 per cent aqueous solution of quinine dihydrochloride as the unpalatable substance for the models, only models and edibles were given to the experimental birds. Bird A pecked three models and ate one, but touched none further in these trials. Similarly, bird B learned after eating one and pecking the next that the models were unpalatable and did not touch the rest of the ones given in these trials. Bird C, apparently more sensitive to quinine, had found the models unpalatable earlier when they were dipped in 20 per cent solution. In all eight trials with a 66 per cent solution, this bird did not touch the models, and hence had already learned to reject them on sight alone. However, it also rejected three edibles on sight during this period which shows it had not yet learned to associate the color of the band on the mealworms with their palatability.

The control bird, D, ate all the mimics and edibles presented throughout the entire series, showing that both green-banded and orange-banded mealworms dipped in distilled water were palatable.

Following these eight trials, the four Starlings were offered ten per cent, 30 per cent, 90 per cent, and 100 per cent mimics (control), respectively. Thus bird A got one mimic in every ten trials. At irregular intervals this bird, and bird B which was given 30 per cent mimics, pecked the green-banded mealworms (models or mimics) although usually did not touch them. This learning behavior is similar to that shown by the Scrub Jays in the earlier mimicry experiments (Brower, 1958a, b), and again indicates that although the model is unpalatable and not eaten, the birds occasionally renew their experience with it, that is, make an "error" by pecking it. On the other

hand at trials 42 and 107, bird A pecked a mimic and ate it. However, in 14 other trials, the mimic was not touched. Bird A ate the edibles in all trials.

Again, bird B which received 30 per cent mimics, or three in each ten trials, pecked models occasionally, but did not even touch most of them. At trial 25, it pecked and killed a mimic, but its behavior indicated that it associated the green-banded mealworm with unpalatability. The other 19 mimics offered were not touched. After trial 66, this Starling would no longer eat the edibles, pecking and leaving several over a period of three days, with the result that experiments with this bird were ended prematurely.

Having seen that experimental populations of ten per cent and 30 per cent mimics were relatively spared from predation, one can now compare these with the results for bird C which got 90 per cent mimics, nine in every ten trials. The deterrent effect of the initial trials with 20 per cent quinine already mentioned, lasted not only through the eight preliminary ones with 66 per cent solution, but into the proportion experiments. For 20 trials, no green-banded mealworms were touched; two models and 18 mimics escaped predation, whereas all 20 edibles were eaten, as well as all subsequent ones given to this bird. At trial 21, a mimic was pecked, at 22 another was eaten. However, in the next three trials one model and two mimics were not touched. From then on, most mimics were eaten, and the one model in each ten trials was usually pecked. At trial 51, a model was not touched, apparently because it followed a model which was pecked at trial 50. At trials 67, 74, 110, and 115, mimics were either pecked or not touched, in three instances one or two trials after the bird had experienced the unpalatable model.

This series of experiments was carried out between 28 January and 10 March 1958.

The second group of Starlings. After the first group of Starlings was released, a new set was obtained in order to present each individual with a different proportion of models and mimics from the outset of the experiments, and in addition to investigate an intermediate proportion between 30 per cent and 90 per cent mimics. Five Starlings appeared to be satisfactory for use in this series and were given the following proportions: ten per cent, 30 per cent, 60 per cent, 90 per cent, and 100 per cent mimics, the last being a control bird. Shortly after the trials began, the control bird would no longer eat mealworms, so that before trials were discontinued with this bird, it had eaten only ten mimics and 11 edibles and pecked and not touched a total of seven of each. The one which got 90 per cent mimics is the nearest to a control for this series. In the statistical analysis, the control bird from the first set was used in comparisons with the second set in so far as it had received only mimics and edibles and had not been subjected to the various distasteful substances.

All four Starlings ate the edibles throughout the experiments. Bird 1 (ten per cent mimics) learned that the model was unpalatable after eating two and pecking one in the first six trials. Thereafter most were not touched, with occasional errors when a model was pecked, or in three instances,

eaten. In the entire series, only one mimic was eaten, at trial 26, but 15 were not touched so that these results were similar to those for bird A (ten per cent mimics) in the first series, in spite of the fact that in that experiment the bird had previously experienced the model.

At first bird 2 (30 per cent mimics) pecked or did not touch models and also mimics, indicating that it was associating the green-banded mealworms with unpalatability, regardless of their actual taste. After trial 55, ten mimics and five models were eaten, but more than half of the mimics in the experiment were not touched.

The new proportion studied in this series was six mimics to four models (60 per cent mimics). Because this bird, 3, was getting more than half mimics, it was thought that perhaps it would peck almost every green-banded mealworm presented, and then finding it palatable in six out of ten trials, would learn to eat the mimics. However, this was not so. It was evident that bird 3 found the models unpalatable; all but one were only pecked or were not touched. Although 18 mimics were eaten, 72 were not touched, and six were only pecked.

As in the first series, bird 4, which was given 90 per cent mimics, ate most of them, showing that if the model is rare enough, mimicry is much less effective. It is interesting to note that periodic rejection of the mimics was closely related to the recent prior presentation of a model. Thus in trials 5, 16, 24, 52, 53, 54, 55, 66, 67, 68, 73, 85, and 97, mimics were not touched, or were pecked or killed, just after the bird had experienced the unpalatable model. There were only 100 trials for bird 4 because this individual was reluctant to eat as many as 20 mealworms per day, and so fell behind the other three birds.

This series of experiments was carried out between 26 March and 22 April 1958.

STATISTICAL ANALYSES OF THE DATA

The first group of Starlings. In so far as the first set of Starlings had a period of conditioning with models which the second did not, the data from the two groups were analyzed separately. Tables 1 and 3 show the reactions of the two groups to mimics. Comparisons within each set were made by the chi-squared method to show whether or not the differences in the reactions of the individual birds to the various proportions of models and mimics were in fact real. The null hypothesis was that there was no difference in the reactions of two Starlings to their respective proportions of mimics. The four necessary 2×2 contingency tables were analyzed by the chi-squared test with the use of the Yates correction factor. Table 2 gives the chi-squared and P values for the first set of four Starlings for the comparison of the number of mimics "not touched—pecked—killed" *vs.* "eaten," that is to say, *not eaten vs. eaten* for each two birds. It can be seen that when the mimics were relatively rare (ten per cent, 30 per cent), there was no significant difference in the number "not touched—pecked—killed" (not eaten) *vs.* "eaten" by the two birds. But between these two and the 90 per

TABLE 1

Data for the reactions of Starlings in group 1 to mimics

	Bird A	Bird B	Bird C	Bird D
Mimics	(10%)	(30%)	(90%)	(100%)
Eaten	2	0	119	160
Killed	0	1	0	0
Pecked	0	0	3	0
Not touched	14	19	22	0
Totals	16	20	144	160

TABLE 2

Comparisons of birds (mimics not eaten *vs.* eaten)	χ^2	P values
Bird A (10% mimics) — Bird B (30% mimics)	= .77, 1 d.f.,	.50 > P > .30
Bird B (30% mimics) — Bird C (90% mimics)	= 56.00, 1 d.f.,	P < .001
Bird C (90% mimics) — Bird D (100% mimics)	= 28.21, 1 d.f.,	P < .001
Bird A (10% mimics) — Bird C (90% mimics)	= 34.73, 1 d.f.,	P < .001

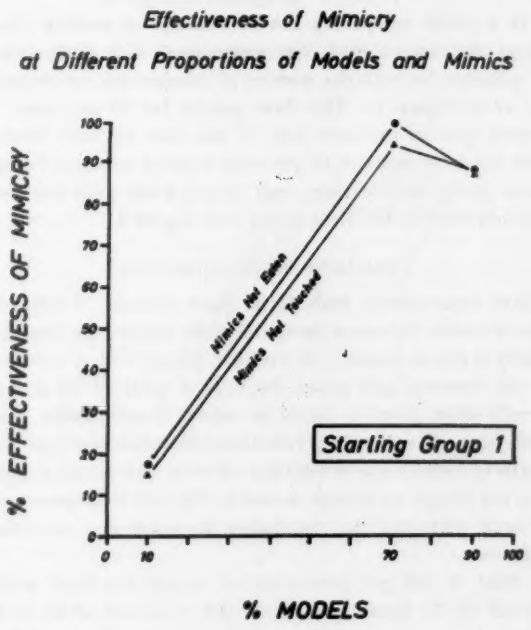

FIGURE 1

cent frequency of mimics, and between the 90 per cent and 100 per cent frequencies, the difference in the number eaten and not eaten was highly significant. This means that although significantly more mimics remained uneaten when they were relatively rare, still when they comprised 90 per cent of the total "population" of models and mimics, significantly fewer were eaten than when 100 per cent mimics was given to a bird.

Figure 1 is a graph comparing the percentage of models and the percentage effectiveness of mimicry, that is, the number of mimics *not eaten* divided by the total number of mimics given to each bird, for the first group of Starlings. It also shows the percentage effectiveness of mimicry when the number of mimics *not touched* was divided by the total given to each bird.

The second group of Starlings. The data for the four Starlings of the second group (tables 3 and 4) were treated in the same statistical manner as in the first set. (It will be recalled that this set of birds was given the proportions of models and mimics from the outset of the experiment in contrast to the first group.) It can be seen that as before when the mimics were relatively rare (ten per cent, 30 per cent), there was no significant difference in the reactions of the Starlings to them. However, it is surprising to note that even when the mimics were at a frequency of 60 per cent, slightly outnumbering the models, the bird did not react in a significantly different way from those which got only ten per cent or 30 per cent mimics. In fact, bird 2 (30 per cent) and bird 3 (60 per cent) failed to eat almost the same percentage of mimics.

Figure 2 is a graph comparing the percentage of models given to these four birds, and the control bird from group one, with the percentage effectiveness of mimicry for both the number of mimics *not eaten* and the number *not touched*, as in figure 1. The three points for 90 per cent, 70 per cent, and 40 per cent models indicate that 80 per cent or more mimics were not eaten. At ten per cent models, 17 per cent mimics escaped being eaten, just as in the first group of Starlings, and 11 per cent were not touched, compared with 15 per cent in the first group (see figure 1).

BEHAVIOR OF THE STARLINGS

As in earlier experiments with Scrub Jays (Brower, 1958), the Starlings showed characteristic behavior patterns when offered an unpalatable model and its visually identical mimic. In the first group, bird A (ten per cent mimics) ruffled its feathers and wiped its beak a total of 13 times out of 160 (eight per cent) when given a model or mimic, considerably less frequently than the Scrub Jays. This Starling sometimes also behaved in a way which indicated a state of indecision or conflict when it was given a model or mimic. It would flap its wings as though about to fly and then preen vigorously or scratch its neck with one foot (probable displacement activities) and not peck the mealworm.

Similarly, bird B (30 per cent mimics) wiped its beak and ruffled its feathers a total of 12 times out of 66 (18 per cent) when it was given a model or mimic, but gave no further visible reaction. For bird C (90 per cent

TABLE 3

Data for the reactions of Starlings in group 2 to mimics

	Bird 1	Bird 2	Bird 3	Bird 4
Mimics	(10%)	(30%)	(60%)	(90%)
Eaten	1	10	18	75
Killed	0	1	0	1
Pecked	0	10	6	4
Not touched	15	28	72	10
Totals	16	49	96	90

TABLE 4

Comparisons of birds (mimics not eaten *vs.* eaten)	χ^2	P values
Bird 1 (10% mimics)—Bird 2 (30% mimics) =	.85, 1 d.f.,	.50 > P > .30
Bird 2 (30% mimics)—Bird 3 (60% mimics) =	0.00, 1 d.f.,	P = 1.00
Bird 3 (60% mimics)—Bird 4 (90% mimics) =	74.94, 1 d.f.,	P < .001
Bird 4 (90% mimics)—Bird D (100% mimics) =	25.50, 1 d.f.,	P < .001
Bird 1 (10% mimics)—Bird 3 (60% mimics) =	.75, 1 d.f.,	.50 > P > .30
Bird 1 (10% mimics)—Bird 4 (90% mimics) =	36.39, 1 d.f.,	P < .001
Bird 2 (30% mimics)—Bird 4 (90% mimics) =	50.46, 1 d.f.,	P < .001

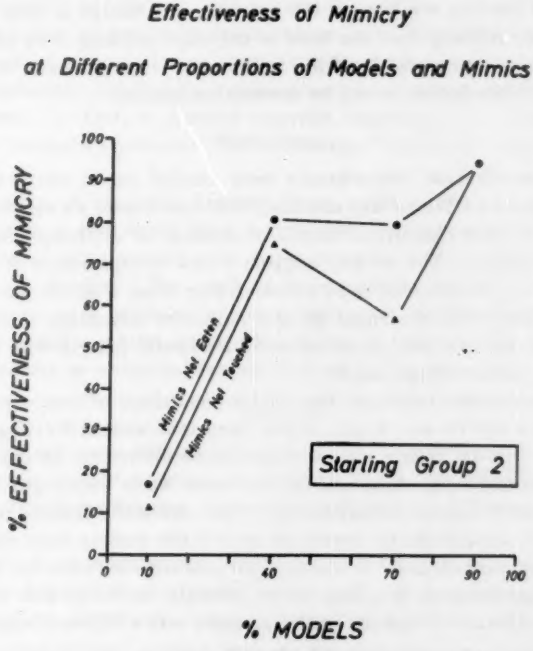

FIGURE 2

mimics) very interesting behavior was observed. This bird gave the feather-ruffling and beak-wiping reactions to the models or mimics in eight out of 160 trials (five per cent). The behavior which was unique to this bird, however, was that of mouthing and rubbing the mimics which followed trials in which a model was offered. This consisted of the bird turning the mealworm with its beak and pressing the insect against the floor of the cage for as long as 40 seconds. It apparently was uncertain of the palatability of green-banded mealworms and tested each before eating it, occasionally to the point of leaving it altogether. During the experiments, this Starling mouthed 26 out of 144 mimics (18 per cent) and also five edibles out of 160 (three per cent), of which it was sometimes suspicious, but nevertheless ate.

Bird D, the control, gave no such reactions to the mimics and edibles all of which were palatable.

In the second group, bird 1 (ten per cent mimics) ruffled its feathers and wiped its beak in 64 out of 160 trials (40 per cent) when a model or mimic was given; bird 2 (30 per cent mimics) in 66 out of 160 (41 per cent); bird 3 (60 per cent mimics) in 13 out of 161 (eight per cent); and bird 4 (90 per cent mimics) in six out of 100 (six per cent). In addition, bird 4 gave this reaction to the edible in six out of 100 trials (six per cent).

Now it has been noted in both groups that when a bird merely pecked or killed a mimic, but did not eat it, a conflict situation was sometimes evident. First, it might be hesitant in seizing the mimic, and then, once it had done so, the Starling would treat the mealworm as though it were an unpalatable model by rubbing it on the floor of the cage, pecking it up and dropping it successively, and feather-ruffling followed by vigorous beak-wiping. The importance of this behavior will be considered below.

DISCUSSION

In this investigation, experiments were carried out in which caged Starlings were used as predators, and modified mealworms as artificial models and mimics to test the effectiveness of mimicry at different proportions of models and mimics. The results suggest a new interpretation of one part of mimicry theory. It has long been assumed that when a mimic outnumbers its model, the mimic will no longer be at a selective advantage because learning predators will not tend to associate the mimetic pattern with the unpalatability of a relatively rare model.

These experiments indicated that under conditions of nearly perfect mimicry, this may not be so. First, it was seen that when a Starling was given 60 per cent mimics, there was no significant difference in the number of mimics rejected by this bird and by two other birds which got 30 per cent and ten per cent mimics, respectively. Thus the birds learned to associate the color with unpalatability nearly as well if the models were slightly more rare than the mimics than if the models greatly outnumbered them. Two other Starlings behaved in a way which strongly indicates that mimicry can be partially effective when the model is quite rare compared with its mimic. These two birds received only ten per cent models, and yet for each, 17 per

cent of the mimics offered was not eaten. There was furthermore a correlation of those which were not eaten with the recent experience of a bird with the model. This suggests that a relatively perfect mimic will derive some protection from predation even if it outnumbers its model by nine to one, and that the mimics spared will most likely be those encountered by a bird soon after it has taken a model. Thus the results of this study show that mimicry may be far more effective under certain conditions in which a mimic outnumbers its model than had previously been expected on the basis of indirect evidence.

A second important finding from these experiments is that with a highly unpalatable model, mimicry may be effective even if mimics are attacked by a predator. In several instances during the experiments, mimics were pecked (and presumably tasted) and yet rejected by Starlings which had had experience with models. That this occurred with an artificial mimic of known palatability is noteworthy because it affords a control on similar behavior shown by the Scrub Jays towards mimic butterflies (Brower, 1958). In the instance of the Viceroy, (*Limenitis archippus archippus* (Cramer)), a mimic of the Monarch, (*Danaus plexippus* (L.)), several were only pecked or killed, and not eaten by the Jays, and at the time it was difficult to assess whether the birds could not discriminate the mimic from the model even after pecking it, or whether in fact the mimic itself was relatively unpalatable. The present experiments give some basis to the alternative that birds which have experienced models can peck a palatable mimic, and yet because they have learned that its particular color-pattern is unpalatable, they will reject it. The learned association of unpalatability with a specific color-pattern is not immediately negated by a *new* association of palatability with the same pattern. In fact, a learned negative response to a visual stimulus appears to dominate a positive "taste stimulus" under the conditions of the experiment.

Another point of similarity between these experiments with Starlings and the previous ones with Scrub Jays is that after learning to avoid the models, both species of birds occasionally made errors by pecking, killing or eating the models (or mimics). That such an error pattern could serve as an adaptive mechanism for a predator to detect changes in the relative frequency of models and mimics in time seems almost certain, and as Fisher (1930) has suggested seems an essential feature of mimicry theory.

SUMMARY

1. Experiments were carried out to test the effectiveness of mimicry at different proportions of models and mimics with Starlings (*Sturnus vulgaris*) as predators and mealworms (*Tenebrio molitor*) as artificial models and mimics.

2. A band of green cellulose paint was used to mark the "model" mealworms which were made unpalatable by being dipped into a 66 per cent solution of quinine dihydrochloride. "Mimic" mealworms were identically

banded, but dipped into distilled water, as were orange-banded "edible" mealworms.

3. It was found that birds which received ten per cent, 30 per cent, and even 60 per cent mimics (the balance being models) rejected about 80 per cent of the mimics by associating their color band with that of the unpalatable model. Mimicry is thus effective when mimics are more frequent than models.

4. Two birds which were given 90 per cent mimics (only ten per cent models) nevertheless rejected 17 per cent of the mimics, indicating that when a model is highly unpalatable, and a mimic relatively "perfect," mimicry may be effective even when a mimic outnumbers its model by as much as nine to one.

5. Under the conditions of the experiment, the selective advantage of mimicry is far greater than believed by previous investigators.

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LITERATURE CITED

Brower, Jane VZ., 1958a, Experimental studies of mimicry in some North American butterflies. I. *Danaus plexippus* and *Limenitis archippus archippus*. Evolution 12: 32–47.

1958b, Experimental studies of mimicry in some North American butterflies. II. *Battus philenor* and *Papilio troilus, P. polyxenes*, and *P. glaucus*. Evolution 12: 123–136.

1958c, Experimental studies of mimicry in some North American butterflies. III. *Danaus gilippus berenice* and *Limenitis archippus floridensis*. Evolution 12: 273–285.

Carpenter, G. D. H., 1949, *Pseudacraea eurytus* (L.) (Lep. Nymphalidae): a study of a polymorphic mimic in various degrees of speciation. Trans. R. Ent. Soc. London 100: 71–133.

1932, Mimicry. Sci. Prog. No. 104: 609–625.

Fisher, R. A., 1930, The genetical theory of natural selection. pp. 146–169. Clarendon Press, Oxford.

Ford, E. B., 1936, The genetics of *Papilio dardanus* Brown (Lep.). Trans. R. Ent. Soc. London 85: 435–466.

Sheppard, P. M., 1959, The evolution of mimicry; a problem in ecology and genetics. Cold Spring Harbor Symp. Quant. Biol. 24: 131–140.

Witherby, H. F., *et al.*, 1938, The handbook of British birds. London.

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AN HYPOTHESIS OF GENE INTERACTION AT THE *S* LOCUS IN SELF-INCOMPATIBILITY SYSTEMS OF ANGIOSPERMS*

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Descriptive data on *S*-allele interactions in angiosperms have been accumulating for several decades. Until now, however, little attempt has been made to provide a theoretical basis for understanding these interactions or to relate them to other features of the self-incompatibility systems in which they occur.

Only self-incompatibility systems that are controlled by multiple alleles at a single locus are considered in the following. They are well described by Brewbaker (1957) and comprise two main types: *gametophytic* systems in which the pollen phenotype is determined by the single *S* allele of a pollen grain, and *sporophytic* systems in which it is determined by the diploid *S* genotype of the pollen-producing plant. The stylar phenotype in both systems is controlled by the diploid genotype. In both systems most individuals are heterozygous at the *S* locus so that, except for the haploid pollen phenotype of gametophytic species, *S* phenotypes are determined almost always by the interaction of two unlike *S* alleles.

Three types of *S*-allele interaction are known: (a) dominance or incomplete dominance of one allele over another; (b) mutual weakening of the activities of the two alleles; and (c) independent action or the apparent absence of interaction. In attempting to understand the physiological significance of these interactions I have used the concepts of gene-controlled reaction rates, threshold effects, limits to gene action, and the competition resulting from limits that were developed by Wright (1941) and Goldschmidt (1955).

The chief function of the *S* locus, from the standpoint of self-incompatibility, is to determine the specificity of incompatibility substances. Each active *S* allele controls the formation of a unique incompatibility substance in the pollen and a corresponding one in the stigma or style. East (1929) suggested that these pollen substances were antigen-like and that the stylar substances were antibody-like. The pollen part of East's hypothesis is supported by serological evidence (Lewis, 1952). Earlier, Lewis (1943) suggested that the incompatibility substances are probably complex molecules whose specificity depends on the pattern of "determinant groups" attached to the basic molecule, and that the action of each *S* allele produces a different pattern of determinant groups. These incompatibility substances are the end-products of the gene interactions under consideration. Unfortunately, little more is known about their chemistry.

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INDEPENDENT ACTION AND DOMINANCE

Independent action is the sole type of interaction found in the styles of both diploids and tetraploids with gametophytic systems. However, in the diploid pollen of gametophytic tetraploids, dominance is much more common than independent action (Lewis, 1947; Brewbaker, 1953; Pandey, 1956). On the other hand, independent action and dominance both occur in the pollen and in the stigmas of sporophytic species (Lewis, 1954). Some sporophytic species, such as Iberis (Bateman, 1954) and Theobroma (Knight and Rogers, 1955) show more dominance than independence, others, like Lesquerella (Sampson, 1958), reveal a preponderance of independent action in heterozygotes.

Basic to the following hypothesis on dominance and independent action is the assumption that if the homozygote $S_1 S_1$ produces the S_1 incompatibility substance and $S_2 S_2$ produces the S_2 substance, then the heterozygote $S_1 S_2$ will produce both S_1 and S_2 substances in the pollen and style. This type of gene action is illustrated by the work of Horowitz and Fling (1956) on tyrosinase production in Neurospora. The two homocaryons each produced a distinct form of tyrosinase, and both forms of the enzyme were found in the heterocaryon.

It seems probable for S heterozygotes that the two substances are not always, if ever, produced in equal amounts. Further, it is assumed that a certain threshold quantity of each incompatibility substance must be produced before incompatibility results. Thus, two substances are present even though mating tests may only detect the dominant one. The amount of a given incompatibility substance that is produced in a heterozygote depends, according to my hypothesis, upon the relative production rates of the two substances and on the duration of production. The occurrence of dominance is taken as evidence that the production systems controlled by the two alleles of a heterozygote compete for a common limiting factor. If the limiting factors were not common, then each allele should be as active as it is in homozygotes. Because the limiting factor is common, production of both incompatibility substances ceases simultaneously when the factor is exhausted. This need not be so, however, when limiting factors are absent and both alleles act independently.

The consequences of this hypothesis become clear when arbitrary numerical values are assigned, as in figure 1. It is assumed that in the pollen (or the style) of the heterozygote $S_1 S_3$, S_1 incompatibility substance forms at the rate (R_1) of two units per hour, whereas S_3 substance forms at the rate (R_3) of one unit per hour. Further, it is assumed for figure 1 that an S allele must produce at least three units of substance before it appears active, that is, before it results in incompatibility. Under these conditions, the apparent activity of each allele depends on the length of time that production continues. For example, in figure 1, if production ceases after two hours, S_1 will be responsible for four units and will appear active, whereas S_3 will be responsible for two units and, not having reached the threshold, will appear recessive. However, if production continues for three hours, both S_1 and S_3

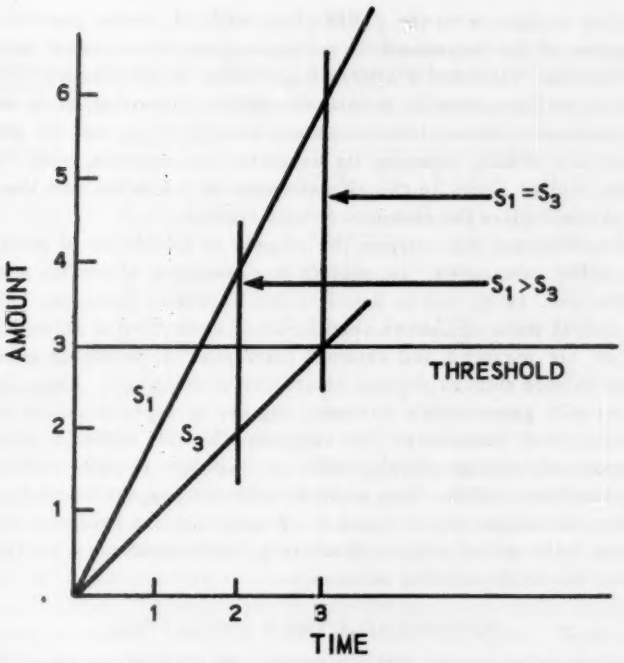

FIGURE 1. Production of two incompatibility substances in the heterozygote $S_1 S_3$. S_1 substance forms at twice the rate of S_3 substance. An allele appears active if it is responsible for a threshold amount of substance when production ceases.

will appear active and independent. Recessiveness thus implies that the production of the incompatibility substance is in some way limited.

An essential feature of this hypothesis is that production of both substances of a heterozygote cease simultaneously when a common limiting factor has been exhausted by the two competing reaction systems. If the final amount of S_1 substance is P_1 units and the final amount of S_3 substance is P_3 units, then the limit (L) to production of both substances is $P_1 + P_3$ units. The amount of substance produced by one allele of a heterozygote depends not only on the level of L, but on the production rate controlled by the second allele of the heterozygote. In the example used in figure 1, $P_1 = L \frac{R_1}{R_1 + R_3}$ and $P_3 = L \frac{R_3}{R_1 + R_3}$. As it seems reasonable to assume that L is constant within a species, different amounts of a specific incompatible substance will be produced by different heterozygotes.

The limiting factor postulated by this hypothesis has yet to be identified. It could be a substrate that is common to the synthesis of both incompatibility substances. If the limit is a substrate, the production curves of figure 1 should be sigmoid rather than linear. Alternatively, it is possible that the two reaction systems compete for a limited number of sites for the in-

compatibility substance on the pollen grain wall. A further possible oversimplification of the hypothesis is the assumption of a common threshold for all *S* alleles. Different *S* alleles might differ in the relative effectiveness of their products (that is, in their thresholds) instead of, or as well as, in their production rates. However, these complications may be added to the hypothesis without changing its essential consequence, which is that dominance implies limits to the effectiveness of *S* alleles, and that independent action implies the absence of these limits.

Some experimental data support the concept of thresholds of activity for incompatibility substances. Incomplete recessiveness of certain alleles in Iberis (Bateman, 1954), and in Brassica and Raphanus (Sampson, 1957a, b) suggest that in these instances near-threshold quantities of incompatibility substances are produced and external conditions or modifying genes can swing the balance through degrees of activity to inactivity. Also, in styles of species with gametophytic systems, degrees of super-threshold amounts of incompatibility substances are suggested by the different degrees to which incompatible tubes carrying different *S* alleles are able to affect self-fertilization (East, 1934). Both sorts of evidence suggest broad thresholds rather than the abrupt one of figure 1. In addition, the evidence also suggests that fully active alleles characteristically produce super-threshold amounts of the incompatibility substance.

DOMINANCE RELATIONS IN A POPULATION

Where dominance occurs, the dominance order of three or more alleles in a population must be considered. This order may be linear or non-linear. With a linear order, if two alleles each act independently of a third they also will act independently of each other. Or, if S_1 and S_2 act independently ($S_1 = S_2$), and S_1 is dominant over S_3 ($S_1 > S_3$), then S_2 also will be dominant over S_3. An example of a non-linear relation is: $S_1 = S_2$ and $S_1 > S_3$ but $S_2 = S_3$.

Most of the data on sporophytic systems follow linear dominance orders. These include findings on Crepis (Hughes and Babcock, 1950), Parthenium (Gerstel, 1950), Iberis (Bateman, 1954), Theobroma (Knight and Rogers, 1954), Cosmos (Crowe, 1954), Cardamine (Lewis, 1954), Capsella (Bateman, 1955), Raphanus (Sampson, 1957a), Brassica (Sampson, 1957b) and Lesquerella (Sampson, 1958). The exceptions involve S_5 in *Brassica compestris* (Bateman, 1955), possibly S_3 S_4 in Iberis stigmas, second series (Bateman, 1954), and possibly S_1 S_2 in Brassica stigmas according to the re-interpretation of Sears' data (Sampson, 1957b). Thompson (1957) definitely established a non-linear dominance sequence in *Brassica oleracea* stigmas where $Sf = Sa$ and $Sa = Se$ but $Sf > Se$ although Se is perhaps incompletely recessive.

Non-linear relations occur in the pollen of artificial tetraploids with gametophytic systems. In Oenothera, Lewis (1943, 1947) found, for example, $S_2 > S_3$ and $S_3 > S_4$ but $S_2 = S_4$. In *Trifolium repens*, Brewbaker (1955) reported that $S_5 > S_8$ and $S_8 > S_6$ but $S_6 > S_5$. However, only linear relations were found in autotetraploid *Trifolium pratense* (Pandey, 1956).

TABLE 1

Change in dominance relations of three alleles as the limit to the production of incompatibility substance is raised. The threshold of activity for each allele is three units.

Genotypes	Production rates	Amounts of incompatibility substances produced			
		L = 6	L = 7	L = 8	L = 9
S_1	$R_1 = 2.0$	$P_1 = 4.00$	4.67	5.33	6.00
S_3	$R_3 = 1.0$	$P_3 = 2.00$	2.33	2.67	3.00
S_1	$R_1 = 2.0$	$P_1 = 3.63$	4.24	4.85	5.46
S_2	$R_2 = 1.3$	$P_2 = 2.37$	2.76	3.15	3.54
S_2	$R_2 = 1.3$	$P_2 = 3.39$	3.96	4.52	5.09
S_3	$R_3 = 1.0$	$P_3 = 2.61$	3.04	3.48	3.91
Dominance relations		1 > 3	1 > 3	1 > 3	1 = 3
		1 > 2	1 > 2	1 = 2	1 = 2
		2 > 3	2 = 3	2 = 3	2 = 3

An important indication of the usefulness of the present hypothesis is its ability to explain the significance of linear and non-linear dominance orders. For this purpose, table 1 gives the amounts of incompatibility substance produced by three alleles acting in the three possible heterozygotes. The amounts of incompatibility substances were calculated from the equations discussed earlier. The table shows how the dominance order depends upon the extent to which L exceeds twice the threshold value. When L equals the minimum amount necessary for two alleles with equal production rates to act independently (in table 1 when L = 6), the dominance sequence will be linear and will reflect production rates exactly. With a slightly higher limit (L = 7), the dominance order will be still linear but alleles with slightly different rates will act independently. With a still higher limit (L = 8), instances of non-linear dominance relations can occur, but when the limit is sufficiently high all alleles will act independently. Thus the hypothesis readily explains linear and non-linear dominance orders in populations.

MUTUAL WEAKENING

Mutual weakening of the activities of both alleles of an *S* heterozygote is known almost exclusively from the pollen of artificial tetraploids with gametophytic systems. This rare type of interaction, which is often termed "competitive interaction," has received more attention than have dominance and independent action. Mutual weakening accounts for instances of self-compatibility in tetraploids of Pyrus (Crane and Lewis, 1942), Petunia (Stout, 1952) and three species of Trifolium (Atwood and Brewbaker, 1953; Brewbaker, 1953; Pandey, 1956). It occurred in two of the 39 pollen *S* heterozygotes studied in *Trifolium hybridum* (Brewbaker, 1953) and in two of the 12 pollen heterozygotes of *T. pratense* (Pandey, 1956). Mutual weakening was detected in three of six pollen heterozygotes of Oenothera (Lewis, 1947) but there the weakening was insufficient to give self-compatibility.

Before Hughes and Babcock (1950) and Gerstel (1950) demonstrated that multiple allelic, sporophytic incompatibility systems do exist, Lewis (1944)

argued that their occurrence was unlikely because they would be handicapped by the mutual weakening interaction. On the contrary, mutual weakening has proved rare among sporophytic systems. The one possible example is S_3 S_4 in Iberis, second series (Bateman, 1954).

Lewis (1943, 1952) offered two hypotheses to explain mutual weakening: (1) that two *S* alleles, in the process of competing for a basic molecule to which they attach specific determinant groups, counteract each other so that part of the base is left undetermined, or (2) that two *S* alleles interact to produce a product with new specificity.

My hypothesis does not explain mutual weakening and, therefore, must be re-examined. The hypothesis assumes that some limit is universal to the action of all *S* alleles of a species. This universal limit could be the basic molecule to which each allele applies a specific pattern of determinant group as Lewis suggested. It is evident, however, that the supply of determinant groups also can be limited and that this second limit might sometimes be reached before the supply of common base is exhausted. This could result in mutual weakening between alleles with like quantitative requirements for determinant groups. This explanation gives the same result as hypothesis (1) of Lewis, but perhaps differs in detail. It demands that the secondary limits in the pollen of tetraploids with gametophytic systems be especially restrictive.

There is evidence to support the hypothesis that mutual weakening results from competition for a second limit. In certain pollen heterozygotes of Oenothera (Lewis, 1947) and Trifolium (Pandey, 1956) in which mutual weakening was insufficient to confer full self-compatibility, dominance also occurred. That is, the activities of both alleles were weakened, but one much more so than the other. Pandey found that the potencies of four alleles for the two interactions were independent. For example, S_2 was dominant over S_1 with no competition, whereas both S_2 and S_1 were dominant over S_3 but with competition. Thus S_3, the weakest allele with respect to dominance, was the strongest in the mutual weakening reaction. Competition for a second substrate readily accounts for the independence of the two types of interaction.

The presence of non-linear dominance orders in the pollen of artificial tetraploids of gametophytic species suggests moderately high limits to *S* allele action. On the contrary, mutual weakening in the pollen of these species suggests restrictive limits. This does not contradict the hypothesis if, as is proposed, the two phenomena reflect the levels of different limits.

DIFFERENCES BETWEEN SPOROPHYTIC AND GAMETOPHYTIC SYSTEMS

Table 2 shows that the two types of incompatibility systems are characterized by different types of allele interaction. Hence, if my arguments are correct, the limits imposed upon *S*-allele activity should differ in the two systems.

Direct comparison of allele interaction in the pollen of sporophytic and gametophytic species is precluded on the diploid level by the haploid pollen

determination in gametophytic systems. On the tetraploid level the data from sporophytic systems are too meager to warrant comparison. Thus we can compare only allele interaction in the pollen of sporophytic diploids with that in the pollen of gametophytic tetraploids. The presence of both independent action and dominance suggests moderate limits in the pollen of sporophytic species. In the pollen of artificial tetraploids with gametophytic systems, on the other hand, the rareness of independent action, the prevalence of dominance and the occurrence of mutual weakening suggest that here the limits are more restricting than in the pollen of sporophytic species.

TABLE 2

S-allele interactions in sporophytic and gametophytic self-incompatibility systems

Type of interaction	Sporophytic		Gametophytic	
	Pollen	Stigma	Pollen	Style
Interactions impossible	...	...	in diploids	...
Independent action	common	common	rare in 4n	universal
Dominance	common	common	common in 4n	absent
Mutual weakening	absent	found once	occasional in 4n	absent
Non-linear dominance relations	absent	present	present	absent

This postulated difference in limits to *S* action in pollen corresponds to the genetical difference between the two systems. Because the incompatibility phenotype of the pollen in gametophytic species is determined by the haploid pollen genotype, the incompatibility substance must be elaborated within the pollen grain itself, sometime after Anaphase I. In sporophytic systems, on the other hand, we know that the haploid genotype of the pollen grain plays no part in determining the specificity of the pollen incompatibility substances. Hence these substances probably are supplied to the developing pollen grain from diploid anther tissue or tapetal fluid. Thus it is conceivable that greater substrate limits are imposed on *S*-allele action in the pollen of gametophytic systems than in the pollen of sporophytic systems.

Further, the differences in pollen limits that are indicated by the differences in allele interaction agree with the conclusions of Pandey (1958) on the different course of pollen development in the two systems. Pandey suggested that, in the sporophytic systems, an excess of metabolites (compared with gametophytic systems) leads both to precocious *S*-allele activity and to an early haploid mitosis that gives trinucleate pollen grains. In gametophytic systems, a relatively smaller supply of metabolites during pollen maturation leads to a delay in *S*-allele activity until after cytokinesis and also to a delay in haploid mitosis, thus giving the binucleate pollen grains characteristic of single locus gametophytic systems.

Considering now the stigmatic and stylar half of the incompatibility mechanism, the presence of both independent action and dominance in

sporophytic systems suggests moderate limits which, however, are high enough to permit a few non-linear dominance orders in populations. In contrast, the universal independent action of alleles in the styles of gametophytic species implies the absence of limits within a detectable range. There is a well-marked correlation between these postulated limits and the site of incompatible pollen tube inhibition. In sporophytic systems, inhibition of pollen germination and tube growth occurs on the stigma surface and several experiments (Sears, 1937; Tatebe, 1939, 1955; Kroh, 1956) show that removal of the stigma top overcomes the incompatibility.

In contrast, the inhibition of pollen tube growth in gametophytic systems takes place over a considerable length of the style. Thus, stigmatic inhibition involving relatively few cells corresponds to the moderate limits postulated for sporophytic systems, whereas stylar inhibition involving a large number of cells corresponds to the postulated absence of limits in the styles of gametophytic systems. The difference in site of pollen inhibition is the strongest evidence available in favor of the postulated limits to *S*-allele activity.

SUMMARY

1. In Angiosperms, the common types of *S*-allele interaction that are found in self-incompatible systems controlled by multiple alleles at a single locus are independent action, partial or complete dominance, and mutual weakening. These are discussed in terms of a reaction system with the following properties: (a) each *S* allele governs the production of a specific incompatibility substance; (b) this substance must be present in a threshold quantity before it causes incompatibility; (c) heterozygotes produce two such substances, one for each *S* allele.

2. Independent action in a heterozygote is believed to result if the limits to production are high enough for each of the two allele-specific substances to be produced in super-threshold quantities.

3. Dominance is explained in terms of unequal competition between the reaction systems controlled by the two alleles for some limited factor. Non-linear dominance relations can occur in populations because super-threshold quantities of incompatibility substances, although unequal, have equal potency in heterozygotes.

4. Mutual weakening is attributed to secondary limits that apply to the activities of only certain *S* alleles.

5. The hypothesis suggests moderate limits to *S*-allele action in the pollen of sporophytic species, but more restrictive limits in the pollen of artificial tetraploids with gametophytic systems. These correspond to the differences in the time of *S*-allele action in the pollen.

6. The postulated moderate limits in the stigmas of sporophytic species correspond to the narrow zone of pollen inhibition. In contrast, the absence of limits in the styles of gametophytic species agrees with the extended zone of pollen-tube inhibition.

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LITERATURE CITED

Atwood, S. S., and J. L. Brewbaker, 1953, Incompatibility in autotetraploid white clover. Cornell Univ. Agr. Exp. Sta. Mem. 319: 1–47.

Bateman, A. J., 1954, Self-incompatibility in Angiosperms. II. *Iberis amara*. Heredity 8: 305–332.

1955, Self-incompatibility systems in Angiosperms. III. Cruciferae. Heredity 9: 53–68.

Brewbaker, J. L., 1953, Oppositional allelism in diploid and autotetraploid *Trifolium hybridum* L. Genetics 38: 444–455.

1955, Incompatibility in autotetraploid white clover. II. Dominance and double reduction. Genetics 40: 137–152.

1957, Pollen cytology and self-incompatibility systems in plants. J. Hered. 48: 271–277.

Crane, M. B., and D. Lewis, 1942, Genetical studies in pears. III. Incompatibility and sterility. J. Genetics 43: 31–43.

East, E. M., 1929, Self-sterility. Bibliog. Genet. 5: 331–370.

1934, Norms, of pollen-tube growth in incompatible matings of self-sterile plants. Proc. Nat. Acad. Sci. 20: 225–230.

Gerstel, D. U., 1950, Self-incompatibility studies in Guayule. II. Inheritance. Genetics 35: 482–506.

Goldschmidt, R. B., 1955, Theoretical genetics. 563 pp. University of California Press, Berkeley, California.

Horowitz, N. H., and M. Fling, 1956, Studies of tyrosinase production by a heterocaryon of Neurospora. Proc. Nat. Acad. Sci. 42: 498–501.

Hughes, M. B., and E. B. Babcock, 1950, Self-incompatibility in *Crepis foetida* (L.) subsp. *rhoeadifolia* (Bieb.) Schinz et Keller. Genetics 35: 570–588.

Knight, R., and H. H. Rogers, 1955, Incompatibility in *Theobroma Cacao*. Heredity 9: 69–77.

Kroh, M., 1956, Genetische und entwicklungsphysiologische Untersuchungen über die Selbststerilität von *Raphanus raphanistrum*. Zeits. indukt. Abst. u. Vererb. 87: 365–384.

Lewis, D., 1943, Physiology of incompatibility in plants. III. Autotetraploids. J. Genetics 45: 171–185.

1944, Incompatibility in plants, its genetical and physiological synthesis. Nature 153: 575–578.

1947, Competition and dominance of incompatibility alleles in diploid pollen. Heredity 1: 85–108.

1952, Serological reactions of pollen incompatibility substances. Proc. Roy. Soc. Lond. (B) 140: 127–135.

1954, Comparative incompatibility in Angiosperms and Fungi. Adv. Genetics 6: 235–285.

Pandey, K. K., 1956, Incompatibility in autotetraploid *Trifolium pratense*. Genetics 41: 353–366.

1958, Microsporogenesis, time of *S*-allele action, pollen cytology and place of inhibition and their relationship with the evolution of gametophytic and sporophytic systems of self-incompatibility. Proc. Xth Intern. Cong. Genetics. 2: 212–213.

Sampson, D. R., 1957a, The genetics of self- and cross-incompatibility in *Brassica oleracea.* Genetics 42: 253–263.

1957b, The genetics of self-incompatibility in the radish. J. Hered. 48: 26–29.

1958, The genetics of self-incompatibility in *Lesquerella densipila* and in the F_1 hybrid *L. densipila* × *L. lescurii.* Can. J. Bot. 36: 39–56.

Sears, E. R., 1937, Cytological phenomena connected with self-sterility in the flowering plants. Genetics 22: 130–181.

Stout, A. B., 1952, Reproduction in Petunia. Memoirs Torrey Bot. Club 20 (3): 1–202.

Tatebe, T., 1939, The effect of the mutilation of stigmas on self-fertility in the Japanese Radish. J. Hortic. Assoc. Japan 10: 62–65. (In Japanese with English summary).

1955, Studies on the self-incompatibility of the common cabbage. II. On inhibiting substance. J. Hortic. Assoc. Japan 24: 168–174. (In Japanese with English summary).

Thompson, K. F., 1957, Self-incompatibility in marrow-stem kale, *Brassica oleracea* var. *acephala.* I. Demonstration of a sporophytic system. Genetics 55: 45–60.

Wright, S., 1941, The physiology of the gene. Physiol. Rev. 21: 487–527.

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NICHE SIZE AND FAUNAL DIVERSITY

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The question, "why are there more kinds of birds in the tropics," can be answered in at least four different ways. These may be classed as historic, geographic, ecologic, and behavioral explanations, though the distinctions are clearly not as sharp as listing them might imply. A detailed consideration of these explanations will be forthcoming at a future date (MacArthur and Klopfer, in preparation), but at the present time it will be of value to consider in just what manner the varieties of birds do vary as one proceeds from regions which undergo marked annual changes in the conditions essential to the survival of birds to regions of marked annual stability. By and large, two extremes of stability and lability can be represented by the tropics and the temperate zones.

RELATIVE NUMBERS OF PASSERINES AND NON-PASSERINES

Of additional interest to the ecologist is the query, "in what manner does diversity change from north to south?" How do the proportions of different groups change? In the case of birds, specifically, is there an increase in both the numbers of passerines and non-passerines or does one increase to a greater extent than the other? This last question is of interest because of two proposals that have been made to explain the greater diversity of the tropical avifauna. One of these proposals involves an increase in the number of species' niches in the tropics, presumably resulting from a more complex (in diversity and stratification) plant community. The other suggests that the greater environmental stability of the tropics would favor more stereotyped behavior patterns (for reasons of efficiency in energy extraction) and thus smaller, more restricted niches would result (Klopfer, 1959; MacArthur, in preparation). By a "smaller niche" we mean that the measurable range of conditions used by A is less than that used by B. The results of this paper give preliminary information on this second hypothesis.

The argument assumes the phylogenetically younger passerines to have a less limited central nervous capacity than the non-passerines and thus to be more capable of modifying their behavior to fit changing environmental stimuli. If true, the passerines should be relatively more abundant in unstable environments. Further, with their less stereotyped behavior, larger niches should result. Therefore, if an analysis of census data were to show that the proportion of non-passerine individuals does not increase towards the tropics, we would have to consider the notion of smaller niches in the tropics unsupported, while the alternative finding would encourage belief in

this claim. A second, though less plausible, possibility is that tropical passerines, as a group, show more highly stereotyped behavior (for example, smaller niches) than non-tropical passerines. Because behavioral plasticity is considered to require a higher order of central nervous organization than stereotypy, no such differences between tropical and non-tropical non-passerines need be considered.

The data of table 1 A show how the proportions of non-passerines change from north to south. By and large, the figures support the conclusion that towards the equator conditions are favorable for the existence of non-passerines to a greater degree than is the case farther north. We conclude that tropical niches may well be smaller than those to the north.

Of course, tropical and temperate areas have had different geologic and climatic histories. However, historical factors could only explain a greater proportion of non-passerines in Mexico than in northern United States and Canada if non-passerines were restricted to the tropics or passerines to the north while speciation was taking place. This may have been the case. However, the pattern of restriction to the tropics of non-passerine land birds is world-wide and suggests that not only physical barriers prevented them from colonizing temperate areas. Instead, it is most reasonable to assume that lack of plasticity in their individual niche requirements prevented non-passerines from exploiting the temperate regions as fully as the passerines. Thus, a study of history only strengthens the case for the tropical birds, as a group, being less plastic. Further confirmation must come from a study of Old World tropical and non-tropical censuses, or from Southern Hemisphere figures. It is interesting to note that South America, with much the richest bird fauna of any continent is also unique in having mostly non-oscine, or more primitive, birds.

MEAN ABUNDANCES OF PASSERINES AND NON-PASSERINES

With a reduction in niche size, that is, increased specialization or behavioral stereotypy, one would predict a reduction in the number of individuals per species for a given area. Where requirements are broad rather than highly specific, that is, the niche is large rather than small, a greater density of individuals of the particular species in question should result. By way of example, consider a bird whose feeding is restricted to a single food-plant (small food-niche). Fewer individuals of this species can coexist in a given area than in the case of a species feeding from a variety of plants. Table 1 B and figure 1 indicate how the number of individuals per species varies between passerines and non-passerines in the tropics and non-tropics.

Since the number of individuals per species varies with the size of the censused plot, the data are tabulated in terms of individuals per species per 100 acres. Even this does not make censuses from very different areas easily comparable, but the following conclusions seem clear: First, the mean abundance (per species per 100 acres) drops towards the tropics for the passerines, more than for the non-passerines. This is seen in figure 1, where

TABLE 1

Region	Habitat	A. Per cent of individuals which are non-passerine*	B. Territorial males per 100 acres per species			References
			Passerine / Non-passerine	Non-passerine	Passerine	
1. Ontario	Northern coniferous forest	6.2	5.76	1.7	9.8	Kendeigh, 1947
2. Maine	Northern coniferous forest	1.2	4.	3.	12.	Kendeigh, 1947
3. Maine	Northern coniferous forest	3.	3.97	3.1	12.3	Stewart and Aldrich, 1952
4. NW Territory	Northern coniferous forest	8.8	3.18	5.	15.9	Stewart, 1955
5. NW Territory	Northern coniferous forest	4.5	4.59	3.4	15.6	Stewart, 1955
6. Idaho	Northern coniferous forest	12.4	1.68	10.8	18.1	Longley, 1944
7. South Dakota	Northern coniferous forest	20.	1.	15.	15.	Whitney, 1956
8. Colorado	Northern coniferous forest (20 acre plot)	30.	.93	7.5	7.	Hering, 1956
9. Colorado	Northern coniferous forest (100 acre plot)	8.8	4.79	3.3	15.8	Thatcher, 1956
10. Colorado	Northern coniferous forest	9.	5.29	0.7	3.7	Thatcher, 1956
11. Oregon	Northern coniferous forest	5.	2.38	5.	11.9	Fables and Fables, 1957
12. North Carolina	Northern coniferous forest	.4	23.77	1.3	30.9	Adams, 1959
13. New York	Northern deciduous forest	8.	3.83	1.8	6.9	Kendeigh, 1946

*Exclusive of ducks, grebes, shore-birds, and other aquatic species.

TABLE 1 (*continued*)

Region	Habitat	A. Per cent of individuals which are non-passerine*	B. Territorial males per 100 acres per species			References
			Passerine / Non-passerine	Non-passerine	Passerine	
14. Ohio	Northern deciduous forest	5.5	6.46	1.3	8.4	Williams, 1947
15. Maryland	Northern deciduous forest	9.8	5.33	8.6	45.8	Stewart and Robbins, 1947
16. Tennessee	Northern deciduous forest	5.4	4.38	5.8	25.4	Aldrich and Goodrum, 1946
17. West Virginia	Northern deciduous forest	2.	4.07	6.7	27.3	DeGarmo, 1948
18. North Carolina	Northern deciduous forest	11.4	2.68	2.5	6.7	Smith, 1959
19. North Carolina	Northern deciduous forest	3.3	3.88	2.5	9.7	Hunt, 1959
20. Georgia	Dry pine	12.5	2.	1.	2.	Fleetwood, 1948
21. California	Coastal redwood	13.3	2.50	9.6	24.	Pugh and Pugh, 1957
22. North Carolina	Hemlock	3.5	2.18	12.5	27.3	Odum, 1947
23. South Carolina	Hammock forest	9.	3.66	3.5	12.8	Mellinger, 1948
24. Illinois	Oak-gum forest	18.	3.66	3.5	12.8	Snyder et al., 1948
25. Georgia	Oak-pine forest	15.	2.07	5.6	11.6	Whitney, 1953
26. Florida	Oak-pine forest	16.7	2.00	8.	16.	Woolfenden, 1958
27. Arkansas	Oak-pine forest	10.7	1.74	3.9	6.8	Holberg, 1957
28. Arkansas	Oak-pine forest	7.1	3.28	5.8	19.	Holberg, 1956
29. Texas	Oak-Savannah	20.	1.76	6.3	11.1	Dixon, 1957
30. Oklahoma	Prairie	0	...	...	7.7	Howell, 1941
31. Wyoming	Prairie	6.	5.68	2.5	14.2	Mickey, 1939
32. Texas	Prairie	14.	1.85	2.	3.7	Allan and Sime, 1939
33. California	Chaparral	6.	4.68	2.2	10.3	Cogswell, 1948
34. California	Desert	35.	.52	14.3	7.4	Hutchinson, 1942

TABLE 1 (*continued*)

Region	Habitat	A. Per cent of individuals which are non-passerine*	B. Territorial males per 100 acres per species			References
			Passerine / Non-passerine	Non-passerine	Passerine	
35. Arizona	Desert	37.5	1.27	2.6	3.3	Hensley, 1954
36. Durango, Mex.	Desert	35.	2.	.7	1.4	Davis and Fowler, 1959
37. Zacatecas, Mex.	Mesquite-pine-oak	21.4	2.20	4.	8.8	Webster, 1957
38. Chiapas, Mex.	Tropical prairie	43.5	1.60	6.5	10.4	Davis and Kincaid, 1954
39. Veracrus, Mex.	Tropical prairie	48.5	1.21	4.2	5.1	Davis and Morony, 1953
40. Veracrus, Mex.	Coastal prairie	31.4	1.01	7.4	7.5	Davis, 1952
41. Qintana Roo, Mex.	Low tropical woods	24.	1.12	6.6	7.4	Davis and Fowler, 1959
42. Veracruz, Mex.	Lowland tropical forest	34.2	1.47	5.8	8.5	Davis and Morony, 1953
43. Chiapas, Mex.	Upland tropical forest	33.3	1.66	5.9	9.8	Davis and Morony, 1953
44. Veracruz, Mex.	Rain forest	35.3	1.48	5.2	7.7	Davis, 1955
45. Chiapas, Mex.	Cloud forest	25.	3.45	3.9	10.	Davis and Davis, 1957

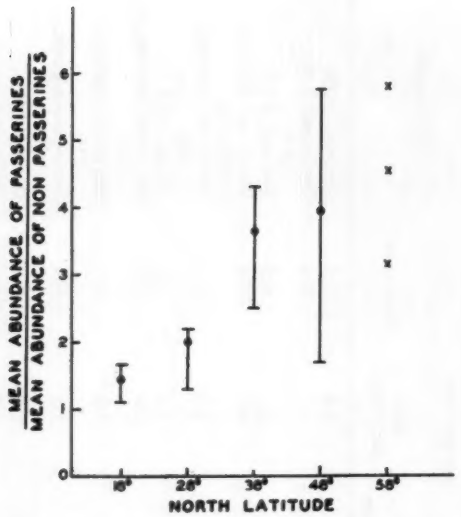

FIGURE 1. Median and 95 per cent confidence interval for median of $\frac{\text{mean abundance of passerines}}{\text{mean abundance of non-passerines}}$ for censuses grouped in 10° intervals from various latitudes. The x refers to values from single censuses.

the ratio, $\frac{\text{mean abundance passerines}}{\text{mean abundance non-passerines}}$, is lower in tropical regions. This suggests that passerine species are more able to expand niches in temperate habitats than are non-passerines. Finally, since the ratio $\frac{\text{mean abundance passerines}}{\text{mean abundance non-passerines}}$ is greater than 0, whatever the latitude, non-passerines have lower mean abundances per species, that is, smaller niches, than passerines. Dr. Elwyn Simons informs us that a similar situation obtains in primates in which specialized primitive species have been confined to the tropics, while plastic, more recent forms are more wide ranging.

SUMMARY

1. As one proceeds from North Temperate regions towards the Tropics, the proportion of non-passerines in the avifauna increases.

2. The number of individuals per species for a given area decreases towards the tropics for the passerines but not for the non-passerines.

3. At all latitudes, however, non-passerines are less abundant than passerines.

This is interpreted as support for the notion that the phylogenetically older non-passerines species are insufficiently plastic in their niche requirements to colonize temperate areas, tropical niches being smaller and less subject to change.

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LITERATURE CITED

Adams, D. A., 1959, Census 9. Aud. Field Notes 13: 464.

Aldrich, J. W., and P. Goodrum, 1946, Census 26. Aud. Field Notes Suppl. Aud. Mag. 146: 144–145.

Allan, P. E., and P. R. Sime, 1939, Census 10. The Season Suppl. to Bird Lore 129: 18.

Cogswell, H. L., 1948, Census 3. Aud. Field Notes 2(6): 226.

Davis, L. I., 1952, Census 38. Aud. Field Notes 6: 324.

1955, Census 27. Aud. Field Notes 9: 425–426.

Davis, L. I., and A. M. Davis, 1957, Census 18. Aud. Field Notes 11: 448.

Davis, L. I., and E. Kincaid, 1954, Census 40. Aud. Field Notes 8: 384.

Davis, L. I., and J. Morony, 1953, Census 30. Aud. Field Notes 7: 351–352.

1953, Census 31. Aud. Field Notes 7: 352–353.

1953, Census 44. Aud. Field Notes 7: 359–360.

De Garmo, W. R., 1948, Breeding-bird population studies in Pocohontas and Randolph Counties, West Virginia. Aud. Field Notes 2(6): 219–222.

Dixon, K. L., 1957, Census 21. Aud. Field Notes 11(6): 450.

Fables, S., and D. Fables, 1957, Census 9. Aud. Field Notes 11(6): 440.

Fleetwood, R. J., 1948, Census 18. Aud. Field Notes 2(6): 238–239.

Hensley, M. M., 1954, Ecological relations of the breeding bird population of the desert biome of Arizona. Ecol. Mon. 24: 185–207.

Hering, L. M., 1956, Census 9. Aud. Field Notes 10(6): 423.

Holberg, A. J., 1956, Census 17. Aud. Field Notes 10(6): 426.

1957, Census 14. Aud. Field Notes 11: 444–447.

Howell, J. C., 1941, Census 7. The Season Suppl. Aud. Mag. 139: 484.

Hunt, R. C., 1959, Census 28: 473.

Hutchinson, A. E., and M. C. Hutchinson, 1942, Census 7. The Season Suppl. Aud. Mag. 142: 19–21.

Kendeigh, S. C., 1946, Breeding birds of the beech-maple-hemlock community. Ecol. 27: 226–244.

1947, Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Ontario Dept. Lands and Forests, Div. Res., Biol. Bull. 1.

Longley, W. H., 1944, Census 27. The Season Suppl. Aud. Mag. 151: 24.

Mellinger, E. O., 1948, Census 20. Aud. Field Notes 2(6): 240.

Mickey, F. W., 1939, Census 7. The Season Suppl. Bird Lore 129: 17.

Odum, E. P., 1947, Census 18. Aud. Field Notes 1(6): 203–204.

Pugh, E., and R. Pugh, 1957, Census 10. Aud. Field Notes 11(6): 440–441.

Smith, W. A., 1959, Census 3. Aud. Field Notes 13: 466.

Snyder, D. P., 1950, Bird communities in the coniferous forest biome. Condor 52: 17–27.

Snyder, D., C. Bonney and W. B. Robertson, 1948, Census 15. Aud. Field Notes 2(6): 237.

Stewart, R. E., and J. W. Aldrich, 1952, Ecological studies of bird populations in northern Maine. Ecol. 33: 226–238.

Stewart, R. E., and C. S. Robbins, 1947, Census 22. Aud. Field Notes 1(6): 211–212.
Stewart, R. W., 1955, Censuses 9, 10. Aud. Field Notes 9(6): 415–416.
Thatcher, D. M., 1956, Census 8. Aud. Field Notes 10(6): 421–423.
Udvardy, M. D. F., 1957, An evaluation of quantitative studies in birds. Cold Spring Harbor Symp. 32: 301–311.
Webster, J. D., 1957, Census 20. Aud. Field Notes 11: 449–450.
Whitney, N. R., 1953, Census 17. Aud. Field Notes 7: 343.
1956, Census 9. Aud. Field Notes 19(6): 423.
Williams, A. B., 1947, Climax beech-maple forest with some hemlock (15 year summary). Aud. Field Notes 1(6): 205–210.
Woolfenden, G., and R. Allan, 1958, Census 15. Aud. Field Notes 12: 450.

LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

ARE THERE NO MAMMAL SPECIES WITH XO MALES—AND IF NOT, WHY NOT?

The recent publication (Matthey, 1958b) of a critical list of 241 species of eutherian mammals for which reliable chromosomal data exist prompts the questions in the title of this note.

If we disregard some ancient and obviously unreliable claims, most of which have been subsequently disproved, there are five species of mammals in which an XO or apparently XO condition in the male has been reported (the remainder all having XY males, except for three or more probably four XY_1Y_2 species, the marsupials *Potorous tridactylus* and *Wallabia bicolor* (?) and the eutherians *Sorex araneus* and *Gerbillus gerbillus*). Three of the five allegedly XO species, namely the rodents *Apodemus speciosus ainu* (2n ♂ = 47), *Clethrionomys bedfordiae* (2n ♂ = 55) and *Microtus montebelli* (2n ♂ = 31), were reported on by Oguma (1934, 1935, 1937), whose cytological determinations are questioned by Matthey. In the case of the first two his doubts seem justified since *Apodemus speciosus speciosus* is stated by Makino (1951) to have 2n ♂ = 48 and three other species of Clethrionomys all have 2n ♂ = 56 (Matthey, 1953a; Makino, 1949). In justice to Oguma it should be pointed out that these are relatively high chromosome numbers which are obviously difficult to determine, and that his work was carried out before the introduction of modern squash techniques, which greatly facilitate cytological observation. Also, the existence of post-reduction of the sex chromosomes in the genus Apodemus, renders the interpretation of the sex chromosome constitution much more difficult than would be the case in any other genus of mammals, with prereduction of the XY pair.

The difficulties of the Apodemus and Clethrionomys material do not exist in *Microtus montebelli*, with the relatively low chromosome number of 2n ♂ = 31 and apparently large chromosomes. Oguma's clear figures of the sex chromosome of this species at meiosis seem to rule out the possibility of a Y being present, as a separate element. On the face of it, *Microtus montebelli* certainly seems to be a species with an XO male (a conclusion with which Matthey agreed in 1949, although in 1958 he was more skeptical).

There exist, however, two other microtine rodents, *Ellobius lutescens* and *Microtus (Chilotus) oregoni*, which have a single sex chromosome in the male and 2n ♂ = 17 in both species (Matthey, 1953b, 1954, 1958a, 1959). In these, however, the female also possesses a single sex chromosome and

the same chromosome number as the male. It was suggested (White, 1957), in the case of Ellobius, that the male has an attached $\widehat{XY}$ condition, the original X and Y having become fused together, and that the female has a similar attached $\widehat{XX}$ chromosome. The system would have to operate as a balanced lethal mechanism, a state of affairs that might have arisen in a mammal producing an excess of ova. This interpretation has been accepted by Matthey (1958a, 1959) and has been extended by him to the case of *Microtus oregoni*, not known to White at the time when he put forward his hypothesis. Although critical evidence (for example, that 50 per cent of the zygotes abort) is still lacking, the cytological conditions, especially in *M. oregoni* (where the single sex chromosome has limbs of equal length in the female and of unequal length in the male) strongly support the hypothesis. Matthey has, however, gone further and claimed that the cytological facts indicate a close phylogenetic relationship between Ellobius and *Microtus oregoni*: that is, that the peculiar sex chromosome mechanism arose once only in the Microtinae. He has been led to this conclusion in part because both species have the same unusually low (for a eutherian mammal) chromosome number.

The taxonomic evidence is not very favorable to this interpretation, however, since Ellobius and Microtus have always been placed in different tribes of the Microtinae. Also the appearance of the sex chromosomes is very different in the two species. Thus we are inclined to the view that the identical chromosome number in the two forms is a mere coincidence and that the strange method of sex determination (if, indeed, it has been correctly interpreted) has arisen independently in these two rodents.

If this is so, the question can be posed as to whether *Microtus montebelli* may not also have an attached $\widehat{XY}$, attached $\widehat{XX}$ mechanism. A re-investigation of this species, by some Japanese cytologist, including a study of the female chromosome set, seems called for. If it turns out to have attached $\widehat{XX}$ and $\widehat{XY}$ chromosomes the question will arise as to whether this condition arose once only or on two or three separate occasions in the Microtine rodents.

An attached-X chromosome in the female would, of course, be inherited directly from a mother to all her daughters without crossing over (except insofar as crossing over might take place between its two limbs).

It is difficult to see how the $\widehat{XX}:\widehat{XY}$ system could have arisen in the first place unless $\widehat{XX}X$, $\widehat{XY}X$ or $\widehat{XX}Y$ individuals were at least occasionally viable and fertile. The $\widehat{XX}:\widehat{XY}$ system could then have arisen by two separate centric fusions or by one centric fusion and a crossover in an $\widehat{XX}Y$ or $\widehat{XY}X$ individual.

If the male of *Microtus montebelli* has an attached $\widehat{XY}$ chromosome rather than a single X, we are led to the conclusion that *no mammal truly lacks a Y in the male sex.* This is what we might expect in view of recent findings that the Y is a powerfully male-determining chromosome in the human species (Ford et al., 1959a, b; Tjio, Puck and Robinson, 1959) and in the mouse (Russell, Russell and Gower, 1959; Welshons and Russell, 1959). We

may conclude that the Y is an indispensable part of the mammalian sex determining mechanism because it is necessary for the development of the male and that it has probably not been lost on any occasion in mammalian evolution.

In groups such as the Coleoptera, where there have been repeated evolutionary "losses" of the Y, we may assume that the functions of this chromosome are or the same nature as they are in *Drosophila melanogaster*, that is to say, it may be necessary for male fertility, but does not have male determining properties as such; thus it would not masculinize individuals that were otherwise female. "Loss" of the Y in such groups is probably not an actual loss but a transfer of most of the substance of this chromosome to the X or to an autosome, by translocation, so that females become homozygous for it. It is this kind of "loss" which we believe is not possible in the mammals.

The existence of three or four instances of XY_1Y_2 species in the mammalia (whereas no X_1X_2Y species is known) may likewise indicate that small portions of the X are more apt to be dispensible in this group than similar segments of the Y (the origin of an XY_1Y_2 mechanism by centric fusion will involve deletion of a segment of the X, while a centric fusion which leads to an X_1X_2Y system involves deletion of a piece of the Y).

LITERATURE CITED

Ford, C. E., et al., 1959a, The chromosomes of a patient showing both mongolism and the Klinefelter syndrome. Lancet 1959: 709–710.

1959b, A sex chromosome anomaly in a case of gonadal dysgenesis (Turner's syndrome). Lancet 1959: 711–713.

Makino, S., 1949, A chromosomal survey in some asiatic species of the Muridae with special regard to the relationship of the chromosomes upon taxonomy. Cytologia 15: 153–160.

1951, Studies on the murine chromosomes. V. A study of the chromosomes in Apodemus, especially with reference to the sex chromosomes in meiosis. J. Morph. 88: 93–126.

Matthey, R., 1949, Les chromosomes des vertébrés. Lausanne, F. Rouge, Librairie de l'Université.

1953a, Les chromosomes des Muridae. R. Suisse Zool. 60: 225–283.

1953b, La formule chromosomique et le problème de la détermination sexuelle chez *Ellobius lutescens* Thomas (Rodentia — Muridae — Microtinae). Arch. J. Klaus Stift. 28: 65–73.

1954, Un nouveau type de chromosomes sexuels chez un mammifère (*Ellobius lutescens* Thomas — Rodentia — Microtinae). Experientia 10: 18.

1958a, Un nouveau type de détermination du sexe chez les mammifères *Ellobius lutescens* Th. et *Microtus (Chilotus) oregoni* Bachm. (Muridés, Microtinés). Experientia 14: 240.

1958b, Les chromosomes des mammifères eutheriens: Liste critique et essai sur l'évolution chromosomique. Arch. J. Klaus Stift. 33: 253–297.

1959, Formules chromosomiques de "Muridae" et de "Spalacidae": La question du polymorphisme chromosomique chez les Mammifères. Rev. Suisse Zool. 66: 175–209.

Oguma, K., 1934, A new type of mammalian sex chromosome, found in a field mouse *Apodemus speciosus*. Cytologia 5: 460–471.

1935, The chromosomes of four wild species of Muridae. J. Fac. Sci. Hokkaido Univ. 4: 35–57.

1937, Absence of the Y-chromosome in the vole, *Microtus montebelli* Edw., with supplementary remarks on the sex chromosomes of *Evotomys* and *Apodemus*. Cytologia, Fujii Jubilee Vol.: 796–808.

Russell, W. L., L. B. Russell and J. S. Gower, 1959, Exceptional inheritance of a sex-linked gene in the mouse explained on the basis that the X/O sex chromosome constitution is female. Proc. Nat. Acad. Sci. 45: 554–560.

Tjio, J. H., T. T. Puck and A. Robinson, 1959, The somatic chromosomal constitution of some human subjects with genetic defects. Proc. Nat. Acad. Sci. 45: 1008–1016.

Welshons, W. J., and L. B. Russell, 1959, The Y-chromosome as the bearer of male determining factors in the mouse. Proc. Nat. Acad. Sci. 45: 560–566.

White, M. J. D., 1957, An interpretation of the unique sex chromosome mechanism of the rodent *Ellobius lutescens*. Proc. Zool. Soc. Calcutta, Mookerjee Memorial Vol.: 113–114.

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NONADAPTIVE ASPECTS OF EVOLUTION

The problems of adaptation are well discussed in numerous places (for example, Simpson, 1953; Dobzhansky, 1951, 1956; Lewontin, 1957; Brown, 1959). The obverse is also of importance, namely, the origin of inadaptive and nonadaptive conditions. There is often a considerable methodological difficulty in determining that a character is not adaptive; often negative evidence is all that can be used. For this reason, and because of the belief in the universality of pleiotropy and the efficiency of selection for minute advantages, Fisher's school considers nonadaptive evolution to be negligible.

Many students, on the other hand, have believed nonadaptive evolution to be of major importance. Most of their examples are spurious, as pointed out especially by Simpson (1953). Perhaps their best documented case is that of an unknown number of phyla (the several hundred "species" are microscopic) of spiriferid brachiopods in the upper Devonian described by Fenton (1931), where there are parallel but different trends toward loss of regularity in minute surface sculpture. Fenton also claims that later individuals in each phylum are less able to repair injuries than were earlier ones. He suggests about five reasons why selection is not an important directing mechanism in these trends:

(1) He sees no advantage in the trends.
(2) The lithofacies (his "environment") does not appear to change.
(3) All the lines become (at least locally) extinct in the time studied, so the trends are not manifestations of other, positively selected, ones.
(4) Diverse forms of different spiriferid species coexist in the same strata.
(5) There are no similar trends in related phyla.

Carter (1951) points out what may be an important fallacy here. "The conditions in which a group is living shortly before its extinction are likely to be unfavorable, for otherwise there would be no reason for the extinction. Degenerate forms are likely to appear at that time." He considers the trends "phenotypic" (that is, environmental) "modifications of body form," due perhaps to relaxation of canalization, or more likely to a secular trend in the environment. Other centrifugal selection is equally possible. Further and rather less probable alternatives are correlated adaptation and actual direct adaptation, for example for less conspicuousness.

Evolutionary trends of the magnitude of that just mentioned are unlikely to be inadaptive or even nonadaptive, if adaptive possibilities exist in the environment. But on a smaller scale this is perhaps not uncommon, particularly in the cases of apparently selectively neutral characters owing their evolution to pleiotropic effects of genes selected for other effects.

Some phenotypes are unambiguously inadaptive. Their presence in some individuals may be the result of mutation or recombination pressure. Buzzati-Traverso (1953) and others have looked with favor and some real evidence on the occasional participation of high mutation rates in directing evolution. This would usually be similar (as far as adaptation is concerned) to the re-

sults of random drift, a probably important effect (also operating differently on different genes). Probable examples of drift in natural populations are those of Epling and Dobzhansky (1942) in the herb Linanthus, and of Lamotte (1951) in the snail Cepaea (agreed to by Sheppard, 1959). Considerable negative evidence is required for proof of drift. The insertion of genes from another population, advantageous there but not so in their new genetic or external environment, by migration (movement of individuals, geographic gradients, introgression) is also possible. This would merely augment the existing mutational polymorphism. Simpson's quantum evolution (1944, to a lesser extent 1953) has relied to a considerable extent on these mechanisms, so the result could be, to paraphrase Goldschmidt (1940), a hopefully monstrous population.

Other characters are adaptively ambiguous. This may be simply because the character itself is adaptive in some respects and inadaptive in others, but favorable overall: a very common situation. A special case of this is where an aspect of the environment toward which the population is adapted, produces exogenously a disadvantageous result. Simpson (1953) gives a possible example by explaining the reported high incidence of bone diseases in cave bears as a byproduct of their dank winter dwellings, although there are alternative explanations for this. Related to this is the ubiquitous situation where the present expression of a trait is the resultant of selective pressures in opposite directions. Body size in many animals has been analyzed in this way in some detail; different expression of the same gene in different genetic backgrounds may also contribute to this general factor. A trait may itself be disadvantageous but be related in some way to other traits that more than offset this: by developmental requirements, by linkage (usually unlikely), by pleiotropy. Allometric growth could be involved in one or more of these aspects. Vestigial characters, now by definition nonadaptive, may once have been functional. Balanced polymorphism makes many individuals relatively inadaptive. Fluctuating environments may reverse selection on a character (for example, seasonal changes in inversions in some Drosophila species). Environmental effects are often nonadaptive, although selection can mold the response of the individual toward an adaptive result.

Differences between groups are often nonadaptive, particularly if one type has not evolved from the other. Simpson (1949) emphasizes this point with respect to the exuberant variety of horns among African antelopes. The presence and (independent) origin of horns are adaptive, but one type is not necessarily better than another.

Natural selection itself can lead to disadvantageous results for the population. This happens regularly in the other components than viability and fertility: meiotic drive (Sandler and Novitski, 1957; Sandler, Hiraizumi and Sandler, 1959) and gametic or gametophytic selection (for example, Crosby, 1949, on wild Primula and probably the T locus in wild Mus, Dunn, 1957 and unpubl.). Sexual selection, intrabrood competition, and other forms of intraspecific competition may lead to the development of characters individually useful but deleterious to the species. Crow and Kimura (1956) give a re-

stricted hypothetical but possible case where the selective value of an allele is lowered as it increases in frequency. Fisher's theory of the evolution of dominance (1930) includes selection for recessiveness of deleterious dominants. This is advantageous to the individual heterozygotes, but the gene is now more common in the population, since it is now mostly homozygotes that are eliminated, and the same absolute number removed are necessary to balance mutation. The reverse case, where a character advantageous to the population is selected for despite being disadvantageous to the individual, is also known. This altruistic selection is probably of little importance except among social insects with a neuter caste; it may occur elsewhere in more social organisms or rarely as a result of nonadaptive fixation in one deme and gene migration to induce interdeme selection. Senescence, of manifest disadvantage to the individual, seems usually to be the result of selection for pleiotropic genes advantageous in youth (Williams, 1957).

A shift in the environment may make previously adaptive characters now deleterious. Adaptation to this change may be low, for any of several reasons: low available genetic variability, high developmental canalization, rapidity of environmental change, the limits on rates of selection. Haldane (1957), in discussing this latter, shows that there is a rather narrow limit on the number and intensity of genes (including modifiers and polygenes) that can be selected for at one time. This may be of considerable importance as a regulator of evolutionary rates, although of course other relations are involved here also. It is also possible that none of the above four conditions are fulfilled, and yet the genetic routes to an adapted genotype all pass through genotypes that are too poorly adapted to survive. Wright's adaptive "surface" is excellently illustrated by the guinea pig (Wright, 1956), where there are at least five genotypically distinct ways to get the wild type hair color. To get from any one to another, at least one other coat color must intervene, which may be sufficiently disadvantageous to prevent this crossing of the valley between them.

SUMMARY

Mechanisms are discussed by which both individuals within a population and evolving groups themselves can develop phenotypes (or modal phenotypes) not in every way adaptive to their environments. This, however, seems subsidiary in importance to adaptive evolution.

LITERATURE CITED

Brown, W. L., 1959, General adaptation and evolution. Syst. Zool. 7 (for 1958): 157–168.

Buzzati-Traverso, A. A., 1953, On the role of mutation rate in evolution. Atti del IX Cong. Intern. di Genet. 1: 450–462.

Carter, G. S., 1951, Animal evolution: a study of recent views of its causes. Sidgwick and Jackson, London, England.

Crosby, J. L., 1949, Selection of an unfavorable gene complex. Evolution 3: 212–230.

Crow, J., and M. Kimura, 1956, Some genetic problems in natural populations. Proc. of the III Berkeley Symp. on Mathematical Statistics and Probability 4: 1-22.

Dobzhansky, Th., 1951, Genetics and the origin of species. Columbia University Press, New York, N. Y.

1956, What is an adaptive trait? Amer. Nat. 90: 337-347.

Dunn, L. C., 1957, Evidence of evolutionary forces leading to the spread of lethal genes in wild populations of house mice. Proc. Nat. Acad. Sci. 43: 158-163.

Epling, C., and Th. Dobzhansky, 1942, Genetics of natural populations. VI. Microgeographic races in *Linanthus parryae*. Genetics 27: 317-332.

Fenton, C. L., 1931, Studies in the evolution of the genus Spirifer. Pub. Wagner Free Inst. Sci. 2: 1-436

Fisher, R. A., 1930, The genetical theory of natural selection. Clarendon Press, Oxford, England.

Goldschmidt, R., 1940, The material basis of evolution. Yale University Press, New Haven, Conn.

Haldane, J. B. S., 1957, The cost of natural selection. J. Genetics 55: 511-524.

Lamotte, M., 1951, Recherches sur la structure genetique des populations naturelles de *Cepaea nemoralis* (L.). Bull. Biol. de France et de Belg. Suppl. XXXV: 1-239.

Lewontin, R., 1957, The adaptations of populations to varying environments. Cold Spring Harbor Symp. Quant. Biol. 22: 395-408.

Sandler, L., Y. Hiraizumi and I. Sandler, 1959, Meiotic drive in natural populations of *Drosophila melanogaster*. I. The cytogenetic basis of segregation-distortion. Genetics 44: 233-250.

Sandler, L., and E. Novitski, 1957, Meiotic drive as an evolutionary force. Amer. Nat. 91: 105-110.

Sheppard, P. M., 1959, Subsequently unpublished discussion of M. Lamotte's paper. Cold Spring Harbor Symp. Quant. Biol. 24.

Simpson G. G., 1944, Tempo and mode in evolution. Columbia University Press, New York, N. Y.

1949, The meaning of evolution. Yale University Press, New Haven, Conn.

1953, The major features of evolution. Columbia University Press, New York, N. Y.

Williams, G. C., 1957, Pleiotropy, natural selection, and the evolution of senescence. Evolution 11: 398-412.

Wright, S., 1956, Modes of selection. Amer. Nat. 90: 5-24.

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THE STRUCTURE OF THE "PEARL" EYE OF *LATHETICUS ORYZAE*

It was reported by Sokoloff in this journal and elsewhere (Sokoloff, 1959a, b, c) that a dissection of the eye of the "pearl" mutant of *Latheticus oryzae* indicates the absence of the retinula in the central region and its development on the periphery only. This conclusion was drawn from the examination of *in toto* preparations, made under the dissecting microscope, and was not based on histological sections. The preparations showed the wild type eye as a solid dark spot, while the "pearl" eyes were transparent in the center and pigmented only on the periphery. Assuming that the pigment indicates the presence and location of retinular elements it seemed as if the mutant eye would have retinulae only on the periphery, although corneal facets were found to be perfectly normal in shape, size and arrangement over the whole eye.

As such a situation seemed to be contrary to all that is known about the morphogenesis of insect eyes (see Bernstein, 1953; Wolsky, 1956) and especially contradicted the earlier findings (Wolsky, 1938) that normal development of corneal facets is closely associated with normal development of the retinula, it was decided (after preliminary correspondence with, and the consent of, Dr. Sokoloff) to reinvestigate the problem on the basis of histological preparations of the wild type and "pearl" eyes in *Latheticus oryzae.* These were made by the junior author using alcoholic Bouin (Duboscq-Brazil) fixative, paraffin mounting and ten micron sections, stained with Heidenhain's iron alum haematoxylin. The insect material was kindly supplied by Dr. A. Sokoloff.

An examination of the sections (figure 1) has revealed at once that the structure of the retinula is perfectly normal in the "pearl" eyes and does not differ in any detail from the normal eye, except in the lack of pigment. In both the wild type and the "pearl" mutant each ommatidium consists of a corneal lens, which has a convex outer and a concave inner surface and is the product of the corneagen cells (primary pigment cells). Under the lens there is a large pseudocrystalline body (pseudocone), formed of four cells, and a retinula, composed of seven visual cells. The visual cells form together a shallow goblet, which bears in its center the photoreceptors (rhabdom). Between the ommatidia there are thin, elongated, spindle-shaped interommatidial cells and in the normal eye both these and the elements of the ommatidia (primary pigment cells and retinular cells) contain numerous dark pigment granules. This situation is almost exactly the same as that described by Marshall (1927) in great detail for the eyes of the closely related species *Tribolium confusum.* In the "pearl" eye of Latheticus the pigment is missing entirely both from the ommatidia and the interommatidial cells, but otherwise the structure is not different from that of the wild type eye.

The question of the nature of the pigmented ring on the periphery of the "pearl" eye was clarified recently by Graham (1957) for the phenotypically identical "pearl" mutant of the related species *Tribolium confusum* and by

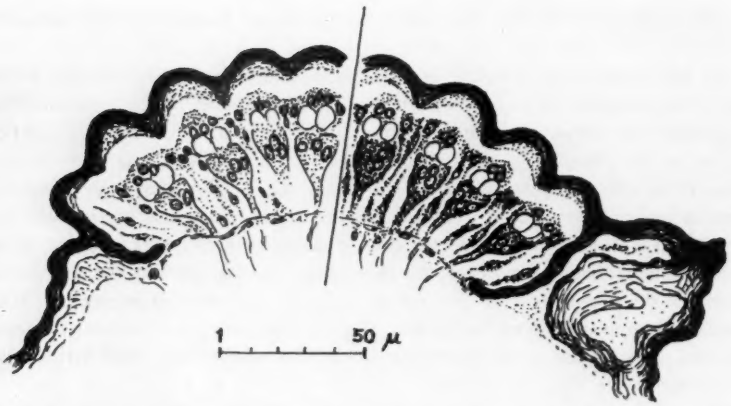

FIGURE 1. Semi-diagrammatic drawing of cross sections through the normal (right) and "pearl" (left) eye of *Latheticus oryzae*, each representing about one-half of the full cross section. Based on photomicrographs. (On right side the section goes through the base of the antenna.) Note complete identity of structure but difference in pigmentation. Note also chitinous ocular sclerite surrounding the eye. Magnified cca 400×.

Sokoloff (1959c) for the "pearl" and the newly found "red" mutants of *Latheticus oryzae*. Sokoloff, on the basis of his further findings, has revised and re-interpreted his earlier statements and admits now the existence of a retinula in the whole "pearl" eye of Latheticus. Both authors find that the black pigmented ring is not caused by any pigment in the eye but by a circular ridge of the chitinous skeleton of the eye capsule, which serves as support for the soft tissues of the eye. This ocular diaphragm is, like the rest of the integument, pigmented and is present both in the wild type and the mutant eye. But in the wild type its presence is concealed by the pigmented elements of the eye proper, while in the "pearl" mutant (as well as in the new "red" mutant) it shows up clearly through the transparent eye tissue and gives the impression that the peripheral ommatidia contain dark pigment, whereas the center is colorless or red.

This situation resolves the apparent difficulty of finding an explanation for the existence of differently pigmented ommatidia side by side. (First it was thought that one has to assume the existence of a rate controlling gene, similar to that shown by Ford and Huxley (1927, 1929) in the red-eyed mutant of the brackish-water shrimp *Gammarus chevreuxi*, which would delay dark pigment synthesis and thus prevent pigmentation in the presumably earlier formed central ommatidia. But since the pigment is not in ommatidial elements at all, there is no need to introduce such an assumption.) The fact that the apparent pigmentation of the peripheral ommatidia is actually caused by a structure, which is outside the eye proper gives a perfect explanation. The pigment of the ocular sclerite (as well as that of the whole chitinous integument) is obviously quite different in its origin and chemistry

from the pigment of the eye. Insect eye pigments, especially the dark and yellow ones, belong mostly to the category of ommochromes (Becker, 1942; Butenandt et al., 1954–1956), while the integumental pigment is presumably dopa-melanin. The usually red or pink pigments of insect eyes belong to another category of chemical compounds, the pteridines (see Albert, 1954; Hadorn, 1959; Kühn and Egelhaaf, 1959). Although there is a certain correlation between the synthesis of dopa-melanin and ommochromes (Butenandt, Biekert and Linzen, 1956; Glass, 1957; Rohner and Wolsky, 1957; Rohner, 1959), genes controlling the formation of ommochromes have in general no influence over dopa-melanin synthesis and vice versa.†

LITERATURE CITED

Albert, A., 1954, The pteridines. Fortschr. Chem. org. Naturstoffe 11: 350–403.

Becker, E., 1942, Uber Eigenschaften, Verbreitung und die genetisch-entwicklungsphysiologische Bedeutung der Pigmente der Ommatin- und Ommingruppe (Ommochrome) bei Arthropoden. Z. induktive Abstammungs- u. Vererbungslehre 80: 157–204.

Bodenstein, D., 1953, Postembryonic development. *In* Insect physiology, edited by K. Roeder. pp. 822–865. John Wiley & Sons, Inc., New York, N. Y.

Butenandt, A., U. Schiedt, E. Biekert and P. Kornmann, 1954, Über Ommochrome. I. Isolierung von Xanthommatin, Rhodommatin und Ommatin C aus den Schlupfsekreten von Vanessa urticae. Ann. Chem. Liebigs 586: 217–228.

Butenandt, A., U. Schiedt and E. Biekert, 1954, Uber Ommochrome. III. Synthese des Xanthommatins. Ann. Chem. Liebigs 588: 106–116.

Butenandt, A., U. Schiedt, E. Biekert and R. J. T. Cromartie, 1954, Uber Ommochrome. IV. Konstitution des Xanthommatins. Ann. Chem. Liebigs 590: 75–90.

Butenandt, A., E. Biekert and B. Linzen, 1956, Uber Ommochrome. VII. Modellversuche zur Bildung des Xanthommatins *in vivo*. Z. physiol. Chem. Hoppe-Seylers 305: 284–289.

Ford, E. B., and J. S. Huxley, 1927, Mendelian genes and rates of development in *Gammarus chevreuxi*. Brit. J. Exp. Biol. 5: 112–134.

1929, Genetic rate-factors in Gammarus. Wilhelm Roux' Arch. Entwicklungsmech. Organ. 117: 67–79.

Glass, B., 1957, In pursuit of a gene. Science 126: 683–689.

Graham, W. M., 1957, Pearl eye in the confused flour beetle, *Tribolium confusum* Duval (Tenebrionidae). Entomol. Monthly Mag. 93: 73–75.

Hadorn, E., 1959, Contribution to the physiological and biochemical genetics of pteridines and pigments in insects. Proc. Tenth Internat. Congr. Genetics 1: 337–354.

Kühn, A., and A. Egelhaaf, 1959, Der rote Augenfarbstoff von Ephestia and Ptychopoda ein Pterinpigment. Z. Naturforsch. 14b: 654–659.

Marshall, W. S., 1927, The development of the compound eye of the confused flour beetle, *Tribolium confusum* Jacqu. Trans. Wisconsin Acad. Sci. 23: 611–630.

Rohner, M. C., 1959, The influence of depression of respiratory metabolism by carbon monoxide on the pigment development of the insect eye. Z. Vererbungslehre 90: 257–262.

Rohner, M. C., and A. Wolsky, 1957, The effect of carbon monoxide on the eye pigment development of Mormoniella and Drosophila. Anat. Record 128: 609.

Sokoloff, A., 1959a, The nature of the "pearl" mutation in *Tribolium castaneum* and *Latheticus oryzae* (Tenebrionidae). Anat. Record 134: 641–642,

1959b, The "pearl" gene in *Latheticus oryzae* Waterh. Amer. Nat. 93: 394–396.

1959c, The genetics of "pearl" in *Latheticus oryzae* Waterh. Canad. J. Genetics Cytol. 1: 182–188.

Wolsky, A., 1939, Experimentelle Untersuchungen über die Differenzierung der zusammengesetzten Augen des Seidenspinners (*Bombyx mori* L.). Wilhelm Roux' Arch. Entwicklungsmech. Organ. 138: 335–344.

1956, The analysis of eye development in insects. Trans. N. Y. Acad. Sci. (Ser. 2) 18: 592–596.

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ON DR. BIRCH'S ARTICLE ON POPULATION ECOLOGY

One point made by Dr. Birch in his interesting article (Amer. Nat. 94: 5-24) requires clarification. He says "The tendency of natural selection is to maximize r." This appears to be incorrect. "r" here is effectively the difference between net birth and death rates. Now r varies with the environment and hence with time in a changing situation. It is well known (c.f. Fisher, 1958) that, in natural selection, genotypes with larger values of r are at every instant making larger contributions to future generations than are genotypes with small r. Furthermore, if one genotype replaces the other, the replacing one has, *during the process* a larger value of r. This does not mean, however, that the final genotype in absence of the first will have a higher value of r than the former did alone. An example will make this clear: Suppose genotype A permits shorter cropping of the grass by some grazing animal than genotype B. Then, if food is in short supply, A will replace B and, during the replacement will be increasing in numbers at the expense of B so that its value of r will be greater. This has no necessary connection, however, with the birth and death rates, and hence with the value of r, which could be maintained by either in the absence of the other. In fact it seems quite likely that population B which does not crop too closely may increase at a greater rate when present alone in the grassland, for grass presumably grows faster when it is of some intermediate length. The exact validity of the example is of course not the point; it does demonstrate that natural selection need not increase r. In fact populations which are stable always have the same value of r (zero), at least on the average, and the value of r when a population is in a period of temporary increase may frequently increase by natural selection but does not necessarily do so. That it frequently does increase, is an exceedingly interesting, but empirical, generalization.

LITERATURE CITED

Fisher, R. A., 1958, The genetical theory of natural selection. Dover Publications, Inc., New York, N. Y.

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February 20, 1960

THE AMERICAN SOCIETY OF NATURALISTS

THE FUTURE OF THE AMERICAN SOCIETY OF NATURALISTS

Report of the Committee on Policy

There come times in the lives of all voluntary associations when questions arise as to their purposes and functions and whether the reasons for their existence are valid and sufficient to maintain them. There are at least three occasions on record when those interested in the American Society of Naturalists have faced such questions. One was on April 10, 1883, when 15 biologists met in Springfield, Massachusetts, and decided that such a society was very much needed and founded it. Matters of common interest then were maintenance of museums, collecting and exhibiting, laboratory methods, and methods of instruction in biology in schools and colleges. Forty-seven years later, in 1930, a Committee on Policy submitted its recommendations for changes in the purpose and character of the society. Its function was seen "as a general rather than a specific society," whose members should be chosen both because they had given evidence of "continued research productiveness of high order" but also of "a philosophical interest extending beyond a single research field." It was to embrace all biological fields and have as its purpose (Section 2 of Article I of the Constitution) "the discussion, advancement and diffusion of knowledge concerning the broader biological problems, including organic evolution, thus serving to correlate the various biological sciences into a common philosophy of biology." It was proposed to do this by "serving as a nucleus for biological meetings apart from the American Association for the Advancement of Science in those years when the Association meeting is held far from the usual research centers." It might arrange "for a meeting at Easter time or some other time than during Christmas week," and in addition to the usual smoker, symposium and dinner, might well organize "round tables dealing with borderline subjects" and give "opportunity for the pooling of knowledge and for discussion, rather than . . . the usual type of voluntarily contributed research papers." The chairman of the Committee on Policy which thus reported was fittingly representative of that field which seemed the natural inheritor of the Naturalist tradition—the ecologist, W. C. Allee. His colleagues were the microbiologist, B. M. Duggar, and the physiologist, D. E. Minnich. Their report was adopted at New Orleans, December 31, 1931.

One can infer from the tenor of the report, that conditions had changed since 1883. The formation of many specialized professional societies had generated centrifugal forces to separate biologists, while the meetings of the A.A.A.S., which had to meet the increased organizational requirements, had become so large that small groups like the Naturalists tended to lose their identity in the mass.

These changes continued and intensified in the period following the reorganization of the Naturalists. At the same general meeting of 1931 at

which the report was adopted, the geneticists formed a separate society, and others followed, representing evolution, taxonomy, ecology, growth and development, human genetics and other special interests. The American Institute of Biological Sciences grew up to assume the organizational burden now created by the biologists themselves and in a sense, the earlier history repeated itself. After a few experiments with separate meetings, the Naturalists continued to meet with the larger groups, their annual functions reduced to a dinner, a symposium (usually jointly sponsored by other societies) and a presidential address. Attendance at the annual business meeting dwindled until on occasion the required quorum of 15 members was not present. In 1950, the Society assumed an added function, the editing of the AMERICAN NATURALIST, which had been founded in 1867 but had had no connection with the Society. The Society benefited by this arrangement since it assumed no financial responsibility for the journal. The publisher of the AMERICAN NATURALIST agreed to provide a subscription for each active member at what was then less than half the stated subscription price. Although this was apparently agreeable to the membership, it did not by itself affect the operation of the society, and doubts as to its continuing function continued to be entertained as evidenced by attendance at meetings.

In 1958 a committee was appointed to consider questions of membership, and operation of the society but the meeting at which these matters were to be discussed was so poorly attended that no action was taken.

In February, 1960, this committee was reconstituted and met in New York City on March 11 with all members except one in attendance. Its terms of reference were "to formulate and recommend a policy for the future operation of the Society, the draft report to be circulated to the members of the Society in June, 1960, and presented for discussion and action at the 1960 membership meeting."

After a full discussion, the committee found itself in unanimous agreement that a society with the purposes stated in Article I, Section 2, of our present constitution is needed today even more than when the Constitution was written. The growth and vitality of the professional societies is gratifying to all but these do not give outlet to those interests which transcend the professional and scientific concerns of special fields. There are many scientists who want to cultivate wider intellectual interests, embracing the effects which their work and thought may have upon the culture and society of their time. Questions of peace and war, of government, of state, social and legal institutions, of education, religion, morality and ethics—all these might be considered. It was felt that the Naturalists could provide a forum and a focus for such interests as could not be accommodated in a professional society, and should devote occasional separate meetings to carefully planned programs embracing a variety of viewpoints focused on a common topic.

The committee thus disposed of the first item on its agenda: shall the society continue or withdraw in favor of societies with special scientific interests? by the following recommendation:

1. That the society reaffirm its adherence to the purpose stated in Article I, Section 2, of the Constitution.

2. The society should free itself from the restrictions of Article IV, Section 1, which now reads "The annual meeting shall be held during convocation week unless otherwise ordered by the executive committee." We recommend that this section be changed to read:

Section 1. *Meetings shall be held at such times and places as the executive committee shall order.*

3. The committee considered that present methods of election to membership do not accomplish the desired end of adding to the society those persons otherwise qualified who share and will promote the purposes of the society.

We recommend that Article II, Section 1, of the constitution be rescinded and that Section 1 now read as follows:

"Membership in the society shall be open to persons who have promoted the natural history sciences by original contributions and who have given evidence of interest in its purposes. Nominations of new members may be made by two members of the society, or by the secretary, using forms provided by and returnable to the secretary who shall periodically transmit the names of nominees to the executive committee, which is empowered to elect new members."

We recommend that a new Section 4 be added to Article II to read as follows:

Section 4. *Foreign members, to pay such annual dues as shall be provided in the by-laws, may be elected by the executive committee.*

The above is to effectuate the consensus of the committee that qualified persons not residing in the United States or Canada should be welcomed to membership with dues lower than those for resident members, but sufficient to include subscription and mailing costs of the AMERICAN NATURALIST.

5. The routine business affairs of the society require continuous attention on the parts of the Secretary, the Treasurer and the Editor. As "working naturalists" they should be freed from the routine in order that their attention may be focused on constructive policies for the operation of the society.

It is recommended that the Executive Committee explore means by which routine matters can be handled by a professional management service such as that available from the American Institute of Biological Sciences.

The Committee:

Vernon Bryson (Editor)
M. Demerec (President, 1954)
L. C. Dunn (President, 1960)
G. E. Hutchinson (President, 1958)
Earl L. Green (Secretary, 1960)
A. E. Mirsky (Editoral Board)
Reed Rollins (Vice President, 1960)
William C. Steere (President, 1957)

SECRETARY'S REPORT, 1959

The Society sponsored a symposium: Interactions in Nature: A Symposium on Modern Ecology, arranged by Dr. Arthur D. Hasler, jointly with the Ecological Society of America and the American Society of Limnology and Oceanography, as part of the annual meeting of the A.A.A.S. in Chicago in December, 1959.

The annual business meeting of the Society was held in Chicago, Illinois, at the Morrison Hotel, on December 28, 1959, with Vice President Arthur D. Hasler presiding.

The minutes of the last meeting were accepted as published in the AMERICAN NATURALIST 93: 333–335, 1959.

The Secretary reported that the Nominating Committee (W. C. Steere, chairman, K. V. Thimann, and G. E. Hutchinson) had nominated the following officers:

President (1960)	Leslie C. Dunn
Vice President (1960)	Reed C. Rollins
Treasurer (1960–1962)	Nelson T. Spratt

There were no further nominations and the officers nominated were unanimously elected.

Dr. G. Evelyn Hutchinson was elected an Honorary Member of the Society, on recommendation of the Executive Committee.

Thirty new members were elected from those sponsored by members during the preceding three years. Those who had accepted membership by March 1, 1960, are listed at the end of this report. There are now about 500 active members of the Society.

The Secretary reported that the Executive Committee had accepted the resignation of Professor L. C. Dunn as Editor of the AMERICAN NATURALIST. Dr. Vernon Bryson was appointed as the new Editor for a five-year term, beginning January 1, 1960. The Committee also voted its sincere appreciation to Doctor Dunn for the high quality of editorial perfection he had achieved from the AMERICAN NATURALIST during his editorship of nearly ten years.

In addition, Vladimir Walters, elected in 1958, became a member too late in 1959 to be included in the report of the Secretary for 1958.

The Treasurer's Report was read by the Secretary and accepted.

The Report of the Editor, the AMERICAN NATURALIST, was read by the Secretary and accepted. The Executive Committee, in consultation with the new Editor, Dr. Vernon Bryson, appointed the following members to the Editorial Board (Class of 1962):

John T. Bonner	James F. Crow
Hampton L. Carson	Alfred E. Mirsky

The time and place of the next meeting of the Society was left to the decision of the Executive Committee.

The Executive Committee recommended a change in by-law 7, so that it will read:

"7. Active members shall pay dues of $7.00 per year, including a subscription to the AMERICAN NATURALIST. Honorary Members and Emeritus Members may receive the AMERICAN NATURALIST upon payment of $4.50 annually."

This change was approved by a majority vote.

The meeting adjourned.

Earl L. Green, Secretary

ASN MEMBERS ELECTED DECEMBER, 1959, WHO HAD ACCEPTED MEMBERSHIP BY MARCH, 1960

Dorothea Bennett	Bernard S. Greenberg	Rodolfo Ruibal
Thomas Burnett	Robert W. Hull	Oved Shifriss
Fred R. Cagle	Nathan Kaliss	George D. Snell
Edward H. Coe, Jr.	Ken-ichi Kojima	Richard M. Straw
Carleton S. Coon	Richard S. Miller	A. O. Tantawy
John W. Crenshaw, Jr.	Richard H. Osborne	George Yerganian
Morris Foster	Peter A. Peterson	

REPORT OF THE TREASURER

Balance on hand December 1, 1958	$ 935.85
Income from dues December 1, 1958–December 1, 1959	2,925.00
TOTAL RECEIPTS	$3,860.85
Expenditures December 1, 1958–December 1, 1959	
L. C. Dunn, Editorial Expenses	$ 300.00
549 subscriptions to The American Naturalist	1,921.50
Bruce Wallace, Secretarial Expenses	56.11
G. F. Sprague, Postage	19.83
A.I.B.S. Membership Dues	490.00
Publication of "Records"	624.00
TOTAL EXPENSES	$3,411.44
Balance on hand December 1, 1959	$ 449.41

G. F. Sprague, Treasurer

We, the undersigned, have examined the Treasurer's books, bank deposits, etc., and find the record presented above to be correct.

Sterling B. Hendricks and Haig Derman, Auditors

REPORT OF THE EDITOR

January 1, 1959–December 15, 1959

The rate of receipt of manuscripts increased somewhat during the year. Of 72 manuscripts received, 22 were declined, most of them as too technical for a non-professional journal. Preference was given to theoretical and synthetic papers of which 15 were accepted out of 18 received.

Of the 34 articles and 18 letters to the editors published in the 1959 volume, the largest number dealt with evolutionary problems while those dealing with ecological observations and theory showed a sharp increase over recent volumes. The major part of one issue was devoted to the Society's Symposium on Integrative Mechanisms in Biology.

Since I shall be abroad on leave of absence beginning in June, 1960, and my second term as managing editor will end on December 31, 1960, I have asked the Executive Committee to be relieved of my post on December 31, 1959.

L. C. Dunn, Editor

ADVICE

THE AMERICAN NATURALIST

the purposes outlined on the inside

Material intended for publication

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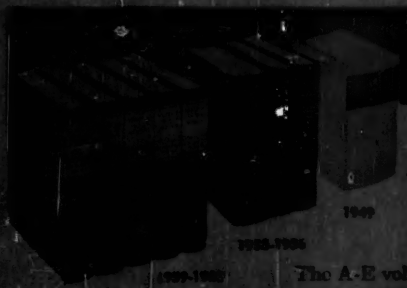

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